Determinants of Species Diversity across Spatial Scales

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For my son, Dorian Aurelius, with love

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ZUSAMMENFASSUNG

Eine der größten Fragen der heutigen Wissenschaft lautet: Was bestimmt Artenvielfalt? Die reine Anzahl an Arten, die auf der Erde existieren, ist atemberaubend. Aber warum gibt es so viele Arten von Lebewesen? Warum gibt es einige Regionen auf der Erde, an der viel mehr Arten vorkommen als in anderen Regionen? Seit dem Beginn der Biogeographie haben sich Wissenschaftler diese Fragen gestellt und versucht sie zu beantworten. Stück für Stück beginnen wir zu verstehen, was die Artenvielfalt auf der Erde und ihre Verteilung bestimmt. Die vorliegende Arbeit trägt im Rahmen dieser übergeordneten Fragen zu unserem wachsenden Verständnis der Artenvielfalt unseres Planeten bei.

Um die Frage zu beantworten, was Artenvielfalt bestimmt, beschäftigt sich diese Arbeit mit dem Aspekt des räumlichen Massstabes. Räumlicher Massstab ist nicht unerheblich, wenn wir versuchen wollen, Artenvielfalt und die sie bestimmenden Faktoren zu verstehen. Wir können beispielsweise die Frage stellen: Warum gibt es in den Tropen mehr Arten als in gemässigtem Klima? Warum gibt es auf großen Inseln mehr Arten als auf kleinen? Dies sind Fragen, die sich ergeben, wenn wir großräumige, regionale Karten von Artenvielfalt betrachten. Andererseits können wir aber auch folgende Fragen stellen: Warum wächst eine Pflanze wo sie wächst, und nicht einfach paar Meter weiter? Warum gibt es beispielsweise in einem Wald Stellen mit vielen Arten und Stellen mit wenigen Arten? Dies sind Fragen, die wir uns stellen, wenn wir die Natur in einem kleinräumigen Massstab betrachten. Das entspräche dem Massstab einer Person, die in einem Wald steht und um sich schaut. Um zu verstehen, was Artenvielfalt bestimmt, müssen wir uns all diese räumlichen Massstäbe anschauen. Weder ist es möglich Artenvielfalt zu verstehen, wenn man nur auf eine Karte schaut, noch ist es möglich sie zu verstehen, wenn wir im Wald stehen und uns lediglich umschauen.

In dieser Arbeit betrachte ich Artenvielfalt in unterschiedlichen räumlichen Massstäben, um besser zu verstehen, wie großräumige Muster der Artenvielfalt kleinräumige Muster beeinflussen. Ich tue dies, indem ich Artenvielfalt sowohl entlang verschiedener Höhengradienten, als auch auf verschiedenen Inseln des südostasiatischen Archipels studiere. Um einer Antwort auf übergeordnete Frage „Was bestimmt Artenvielfalt?“ näher zu kommen, stelle ich drei spezifische Fragen die im Zusammenhang mit dem räumlichen Massstab stehen auf dem wir Artenvielfalt betrachten. 1.) Beeinflusst räumliche Fläche die Unterschiede zwischen groß- und kleinräumigen Muster der Artenvielfalt entlang von Höhengradienten? 2.) In welcher Weise bestimmen großräumiger Artenpool und kleinräumige Unterschiede in Umweltfaktoren die Unterschiede in der Artzusammensetzung von kleinräumigen Artgemeinschaften (β Diversität)? 3.) Ist die Theorie der Inselbiogeographie auf großen wie auf kleinen räumlichen Massstäben gleichwertig anwendbar?

Um Frage 1 zu beantworten habe ich die groß-und kleinräumige Artenvielfalt entlang von fünf Höhengradienten studiert (Kapitel 1). Ich kann zeigen, dass die Fläche in der die großräumige Artenvielfalt aufgenommen wurde für den Unterschied zwischen groß- und kleinräumiger Artenvielfalt verantwortlich ist. Die Fragen 2 und 3 behandele ich durch die Untersuchung der Artenvielfalt von Farnen auf Inseln unterschiedlicher Größe und mit unterschiedlichen Artenpools im südostasiatischen Archipel Indonesiens und der Philippinen. Im Bezug auf die zweite Frage kann ich zeigen, dass die Artenzusammensetzung in kleinräumigen Artgemeinschaften signifikant von der Größe des Artenpools abhängt und dass Konkurrenz zwischen Arten eine Erklärung für die beobachteten Muster liefert (Kapitel 2). Die Ergebnisse

der Untersuchung der dritten Frage zeigen, dass die Theorie der Inselbiogeographie nicht auf allen räumlichen Massstäben gültig ist (Kapitel 3). Der Grund dafür ist, dass der Einfluss des Artenpools sich mit abnehmendem Massstab verringert.
Zuletzt beschäftige ich mich mit einer praktischen Fragestellung, die bei Studien auf kleinräumigen Massstab von Bedeutung ist: Die Benützung von Mossdeckung auf Bäumen als Mass für Relative Luftfeuchte, die häufig eine finanziell und logistisch schwer zu messenden Variable in unzugänglichen Gebieten ist.
Durch diese Resultate komme ich zu der Schlussfolgerung, dass Artenvielfalt von Faktoren bestimmt wird, die bei unterschiedlichen räumlichen Massstäben relevant sind, und es wichtig ist, diese Verknüpfungen im Detail zu verstehen.

SYNOPSIS

One of the biggest questions of today's science is to understand: What determines species diversity? The sheer amount of species on earth is overwhelming, but why? Why do we have so many species on earth? Why do we have some regions on earth which have so many more species than others? Scientists have tried to answer these questions since the beginning of biogeography when it became apparent that species diversity is not equally distributed on earth. Bit by bit we are beginning to understand what determines the diversity of species and why it is so unevenly distributed on earth. This thesis lies on the heart of this question and is a contribution to our growing understanding of the diversity of nature. To help solve the puzzle of species diversity, it focuses on the aspect of diversity across spatial scale. Spatial scale is essential in understanding determinants of species diversity. We might question why we have more species in the tropics than in temperate climates. Why do large islands have more species than small ones? These are questions that arise when we look at maps showing the large, regional scale distribution of species diversity. We might also ask why a plant grows where it grows, and not a few meters beside. How does it happen that at one spot in a forest we see a lot of species and in another spot only a few? A question which arises when we look at diversity at a small, local scale: the scale of a person standing in a forest. To understand species diversity we have to consider all these spatial scales. Neither is it possible to answer what determines species diversity by only looking at a map, nor is it possible by standing in a forest, looking around us. In this thesis I look at species diversity at different spatial scales with attempts to better understand what determines species diversity and how large scale patterns are linked with small scale patterns. I do this by studying the diversity of ferns along different elevational gradients and on different islands of the Southeast Asian archipelago. I ask three specific questions to help build our knowledge about determinants of species diversity across spatial scale. 1) Does area link regional to local diversity along elevational gradients of species diversity? 2) In what way does the regional species pool and local environmental heterogeneity influence local community composition (β diversity) and how are these two aspects linked? 3) the equilibrium theory of island biogeography, is a theory applicable at large scales equally applicable at local scales?

I address question 1 by studying five elevational gradients in the tropics and comparing regional, large scale diversity with local, small scale diversity (Chapter 1). I show that the area at which regional diversity is sampled is mainly responsible for the differences between local and regional diversity. Question 2 and 3 I address by studying the diversity of ferns on islands of different sizes and different species pools in the Philippines and Indonesia. Regarding Question 2 I demonstrate that the species composition of local communities is significantly influenced by the size of the species pool and that competition between species gives a biotic explanation for the observed pattern (Chapter 2). The results obtained by answering question 3 illustrate that the equilibrium theory of island biogeography is not applicable to all spatial scales. The reason for this seems to be that the influence of the species pool is not equally strong across spatial scales (Chapter 3). Finally I answer a practical question regarding the study of species diversity at local scales by providing a proxy for relative air humidity in the tropics: Bryophyte cover on trees (Chapter 4), a financial and logistically challenging variable to measure in the field.

From these answers I draw the conclusion that species diversity is driven by factors operating at different spatial scales and that it is important to understand what links this scales to be able to answer the question, What determines species diversity?

INTRODUCTION

What determines species diversity?

This question has troubled researchers for centuries and has yet to be answered. In 2005 *Science Magazine* named it one of the top 25 questions to be answered by the scientific community in the next century (Pennisi 2005). Answering this question, however, has proven to be difficult due to the complexity of the natural world surrounding us. The question became prominent during the age of enlightenment, in the late 17th century, when scientists started looking outside the bible and onto the rational world for explanations pertaining to the origin of species. Since then the antiquated view of a fixed and steady nature of life on earth gradually gave way to one that was dynamic and ever changing—a shift that would take at least four centuries of accumulating knowledge to complete.

In the mid 18th century, while CARL LINNAEUS (1707-1778) considered his book *Species Plantarum* a fairly good representation of plant diversity on earth, numerous journeys of his in the following decades into tropical regions revealed that most of the species on earth had yet to be documented and described. LINNAEUS himself, however, still did not question the world-view upholding the nature of life as steady and fixed.

It was a few years later, when it became apparent that species diversity wasn't evenly distributed on earth, that GEORGES-LOUIS LECLERC, COMPTE DE BUFFON became one of the first to question the fixity of biota and their paradisiacal origins. By investigating the mammals of Europe and the Americas, he recognized distinct differences in the nature of their faunas: "Those [animals] of one continent are not found in another; or, if there are a few exceptions, the animals are so changed and contracted, that they are hardly to be recognised." (Leclerc 1761). At about the same time, German explorer REINHOLD FORSTER, together with his son GEORG FORSTER, joined the second voyage of JAMES COOK to the southern Pacific Ocean. During his travels through the South Seas, he recognized a tremendous variety in island floras and was one of the first to relate this to the physical characteristics of the islands: "The differences of soil and climate, causes more varieties in the tropical plants of the Southern isles, than in any other." (Forster 1778).

With the turn of the 19th century, ALEXANDER VON HUMBOLT (1769-1835) put these observations into a broader biogeographical context after his journey to America from 1799 to 1804. He recognized the immense amount of species that was entirely restricted to the tropics while absent in temperate climates: "Some forms [of plants], often the most beautiful (Scitaminae, palms, and bamboos), are entirely absent in temperate zones." (Humboldt & Bonpland 1805). These comparisons between tropical and temperate floras contributed to the knowledge of plant distribution, making it more and more apparent that tropical realms harboured more species than the temperate ones, a phenomenon now known as "latitudinal gradient in species diversity." From his climb of Mt. Chimborazo in 1802 sprung yet another striking impression of differences in species diversity; the "elevational gradient in species diversity."

Early research was confined to describing correlations between the environment and flora and fauna, speculating on their causes, until the revolutionary work of CHARLES DARWIN and ALFRED RUSSEL WALLACE (Darwin & Wallace 1858). They introduced a theory of evolution that provided a novel framework giving a causal explanation why species were different from each other and why they differed in geographical distribution: "[A] plant, for instance, would find the best-fitted ground more perfectly occupied by distinct plants in one island than in another, and it would be exposed to the attacks of somewhat different enemies. If then it varied, natural selection would probably favour different varieties in the different islands." (Darwin 1859). WALLACE, as his colleagues FORSTER and DARWIN, based most of his assumptions on island studies. Together they pioneered a new branch of science: island biogeography.

The amount of discovery and impact created by the work conducted on islands was enormous. It was during his travels through the South Seas that FORSTER arrived at his conclusions pertaining to a relation between species and environmental conditions. The theory of evolution benefited greatly from the observations DARWIN made on the Galapagos Islands while on his journey aboard the HMS Beagle. Additionally, WALLACE got his idea of evolution and natural selection while working on the flora and fauna of the Malayan archipelago in 1854 – 1862. This amount of groundbreaking island-based discoveries can be explained by the nature of islands as "natural laboratories": "[Their characteristics of] being discrete, internally quantifiable, numerous, and varied entities, provide us with a suite of natural laboratories, from which the discerning natural scientist can make a selection that simplifies the complexity of the natural world, enabling theories of general importance to be developed and tested." (Whittaker & Fernández-Palacios 2007).

Aside from facilitating the theory of evolution, islands could also ultimately hold the answer to what determines species diversity. In their seminal work *The Theory of Island Biogeography* in 1967, ROBERT MACARTHUR and EDWARD O. WILSON came up with a comprehensive theory about species diversity on islands. They argued that species diversity on islands is mainly influenced by immigration and extinction events leading to an equilibrium number of species (MacArthur & Wilson 1967). Both immigration and extinction are influenced mainly by two factors: isolation of an island, and its size. Since the theory of island biogeography has been published, enormous research has been devoted to how islands can bring us closer to finding what, indeed, determines species diversity.

Gathered from his travels through South America, HUMBOLDT'S observation on the elevational gradient of species diversity got its impetus a bit later than island biogeography. Although HUMBOLDT already recognized the resemblance between elevational and latitudinal gradient of species diversity, studies pursuing this resemblance in more detail would only take place in the early 20th century. JOSEPH GRINELL and TRACY I. STORER were among the first to study elevational distributions of vertebrates, noting changes in their diversity in accordance to elevation. By the mid century, ROBERT H. WHITTAKER began studying the elevational distribution of insects and plants along elevational transects in the United States, a study which eventually lead him to partition diversity into different components (see Page 10) (Whittaker 1960). At the end of the 1970s, the studies of JOHN W. TERBORGH reminded the scientific community of HUMBOLDT'S early observation: that the elevational gradient of species richness mirrors the latitudinal gradient of species richness.

Based on TERBORGH'S studies of Peruvian bird communities, which showed a gradual decline in species diversity towards higher elevations, it was assumed that the elevational gradient mirrored the latitudinal decline in species diversity from the tropics towards arctic climates. For about 20 years the unimodal (humped shaped) trend of diversity that HUMBOLDT, as well as TERBOURGH, showed in his studies were forgotten. There seemed to be much promise in the assumption that broad scale biogeographical patterns—like the latitudinal gradient in species diversity—could be explained only by studying the relatively small spatial extent of an elevational range. By then observations seemed to confirm assumptions that species diversity was mainly dependent on climate and productivity, as both showed a linear response to elevation and latitude. It was CARSTEN RAHBEK who corrected this simplified assumption of a similarity of elevational gradients with the latitudinal gradient in 1995 (Rahbek 1995). He showed that only a small fraction of elevational gradients showed the assumed gradual decline in species diversity with elevation. Furthermore, he stressed that a difference in sampled areas correspondingly gave rise to differences in the perception of elevational gradients of species richness: "When landbird data from tropical South America, compiled at a regional scale using countries as units, are standardized for area, the relationship between species richness and elevation gives a hump shaped curve." (Rahbek 1995). This observation eventually led MICHAEL KESSLER to the conclusion that species diversity along elevational gradients was influenced by the area sampled and that different patterns emerged depending on the spatial scale of the study: "Because land surface area typically declines with increasing elevation …, and because regional area directly influences the regional species pool …, regional richness may be expected to be relatively higher at lower elevations than local richness." (Kessler et al. 2009).

KESSLER'S abovementioned statement carries two important elements in the studies of species diversity: Spatial scale ("regional & local diversity") and the species-area relationship ("land surface area"). Both are of distinct importance in the studies of species diversity and build an integral part of this thesis—hence, they shall be explained in more detail below.

Spatial scale tends to be a confusing concept throughout. Easily confused with the spatial extent of a study, it is closer to the so-called "grain size" of a study, which is used synonymously with spatial scale (Whittaker et. al. 2001). Therefore, it should be noted that "spatial scale" or "scale" in this dissertation uses the definition given by ROBERT J. WHITTAKER in 2001: " Spatial scale[:] should refer to the size of the base unit used in sampling and analysis…" (Whittaker et al. 2001). Following this logic, a regional scale would be a large scale, a local scale would be a small scale. In 1987 ROBERT E. RICKLEFS already mentioned how important it was to include spatial scale in studies of species diversity. During this time his studies focused on the control of regional (large scale) diversity on local (small scale) diversity. He stressed that local diversity strongly depended on regional diversity: "…[E]cologist have sought to explain differences in local diversity by the influence of the physical environment on local interactions among species... But diversity of the biological community often fails to converge under similar physical conditions, and local diversity bears a demonstrable dependence upon regional diversity." (Ricklefs 1987). A few years later SIMON A. LEVIN wrote an influential article about the problem of pattern and scale in ecology, stressing that "… we must find ways to quantify patterns of variability in space and time, to understand how patterns change with scale…" (Levin 1992).

Although he referred to a number of different ecological patterns, the article included patterns of species diversity as well.

A great dearth of data made it difficult for scientists to carry out the conviction that spatial scale had to be incorporated to understand species diversity. It was because of this that only a few scientists made attempts to study species diversity across spatial scales.

In 2001 KATHERINE J. WILLIS and ROBERT J. WHITTAKER recognized that the problem of spatial scale was still imminent and that many studies kept implying that mechanisms explaining species diversity applied equally at all scales: "Much attention, …, has been given to finding the mechanism that explains patterns of species richness, with the underlying assumption that whatever scale the relationship is measured at can be scaled up or down in simple fashion." (Willis & Whittaker 2001). That same year CARSTEN RAHBEK and GARY R. GRAVES published a study investigating bird distributions in South America, giving an empirical example that species diversity was driven by different mechanisms at different spatial scales (Rahbek & Graves 2001). Studying plant diversity across spatial scales, MICHAEL CRAWLEY arrived at a similar conclusion (Crawley & Harral 2001). Regardless of the great challenges posed by studying diversity across spatial scales, these studies made it more and more apparent that the problem of spatial scale was fundamental and definitely not to be overlooked in the pursuit of the question, "What determines species diversity?"

A simple idea ROBERT H. WHITTAKER had in 1960 only exacerbated what was already the arduous task of studying species diversity across spatial scales. Investigating vegetation in the Siskiyou Mountains, he suggested distinguishing three different aspects or levels of diversity: "(1) The richness in species of a particular stand or community… which may be designated primary or 'alpha' diversity. (2) The extend of change of community composition, or degree of community differentiation, in relation to a complex gradient of environment, or a pattern of environments, which may be designated secondary or 'beta' diversity. (3) The species-diversity of a number of community samples, for some range of environments, which have been combined, so that the diversity value is a resultant of both alpha and beta diversities of these samples." (Whittaker 1960).

This separation of diversity components has become increasingly popular in the present day with a wide range of applications. However, while alpha (α) and gamma (γ) are rather straightforward measures of diversity, beta (β) diversity is volatile to confusion. After the years in which WHITTAKER published his idea of β diversity, an enormous amount of indices had been named β diversity.

In 2010 HANNA TUOMISTO needed 44 pages to summarize and explain the sheer number of indices that had accumulated over the years. More importantly, she pointed out that not all of them measured the same thing: "The term *beta diversity* has been used to refer to a wide variety of phenomena. Although all of these encompass some kind of compositional heterogeneity between places, many are not related to each other in any predictable way." (Tuomisto 2010). Confusion surfaced 15 years after WHITTAKER published his initial idea of α, β and γ diversity. MARTIN CODY redefined WHITTAKER'S definition of beta diversity as "the rate of compositional turnover along a habitat gradient within one geographical region" (Cody 1975). Two years later

WHITTAKER accepted and expanded on CODY'S definition by introducing delta and epsilon diversities (Whittaker 1977). All this made it hard for the scientific community to agree on which quantitative interpretation of β diversity to accept (Tuomisto 2010). Nevertheless, the concept to partition species diversity into different components has proven valuable in studying species diversity across scales. Regional diversity is often used synonymously with γ diversity and local diversity is synonymously to α diversity. Linking regional (γ) diversity to local (α) diversity, β diversity could prove to be the key element in studying species diversity across spatial scales and ultimately unlock the mystery behind what determines species diversity.

Having elaborated on spatial scale and diversity partitioning, I'd like to come back to the second important element in the studies of species diversity, which MICHAEL KESSLER mentioned in his 2009 book chapter: "Area."

The relationship between area and species diversity, the "species area relationship" has often been cited as one of ecology's few laws: "You will find more species if you sample a larger area. That rule has more evidence to support it than any other about species diversity." (Rosenzweig 1995). HEWETT C. WATSON was first in discovering this relationship, while investigating plant species richness in Britain in 1859 (Watson 1859). It was, however, OLOF ARRHENIUS who first quantified the species area relationship using the formula: "$y/y_1=(x/x_1)^n$ where x is the number of species growing on the area y, and x_1 that on y_1; n is a constant" in 1921 (Arrhenius 1921). This formula has since then been modified and is today commonly used as $S = cA^z$, with S being the number of species, A being the area, c and z being constants. As early as then, the species area relationship received a great amount of attention, making it apparent that area had different effects on species diversity. It remains to be said, however, that area by itself does not determine species diversity; it is, rather, an indirect factor relating to different mechanisms that change with area, all influencing species diversity.

Species area relationship can be caused mainly by three different underlying mechanisms that CONNOR & MCCOY already mentioned in 1979. They initially explained the increase in species diversity with area: "The 'habitat-diversity hypothesis,'… [which] proposed that as the amount of area sampled is increased new habitats with their associated species are encountered, and thus the species number will increase with area." (Connor & McCoy 1979). A second explanation can be derived directly from MACARTHUR and WILSON'S *Theory of Island Biogeography*: "Immigration rates are assumed inversely proportional to population sizes, which in turn are assumed directly proportional to area. Thus, if distance is held constant population sizes in small areas should be relatively small…implying high probabilities of species extinction: while population sizes in large areas should be relatively large…" (Connor & McCoy 1997). Nevertheless, they also mention a third possible hypothesis: "species number is controlled by passive sampling from the species pool, larger areas receiving effectively larger samples than smaller ones, and ultimately containing more species." (Connor & McCoy 1997).

These three distinct hypotheses, however, don't have to be mutually exclusive. All mechanisms might contribute to the increase in species diversity with increasing area. Aside from the direct increase in species diversity with increasing area, area can also have an indirect effect on species diversity. The surrounding area can lead to a correlation between area and local

diversity even if local samples are of equal size. MICHAEL L. ROSENZWEIG and YARON ZIV called this indirect effect of area on local species diversity the "echo pattern" of regional diversity.

TOM S. ROMDAL and JOHN-ARVID GRYTNES revitalized this idea in 2007 by applying the theoretical assumptions of ROSENZWEIG and ZIV to elevational gradients, calling it an "indirect area effect" (Romdal & Grytnes 2007). Both the echo pattern and the indirect area effect basically describe the same mechanism: the influence of a local community from the regional community surrounding it. This regional community builds the species pool from which local communities are assembled, which increases with area. However, the definition of the species pool differs somewhat from that of regional diversity or gamma diversity (which I mentioned earlier).

Since species pool is an important component of this thesis, I have to stress its difference with regional (γ) diversity to avoid any confusion. These two are only synonymous with each other at certain spatial scales. The species pool is "the set of species that could potentially colonize and establish within a community." (Lessard et al. 2012). Regional diversity (or gamma diversity) in contrast only measures the species actually occurring in a given region, without including the 'potential' species. Area might be a good surrogate for the species pool since it strongly correlates with the number of species in it. However, whatever one might use to explain the echo pattern—be it area, regional diversity, or the species pool—the "echo pattern" linking regional (large scale) diversity to local (small scale) diversity might explain differences of species diversity across spatial scales, and might help in finding a definite answer to what determines species diversity.

While the early studies of WALLACE, DARWIN, FORSTER, HUMBOLDT, and LINNÉ were still generalist in nature and covered a wide range of organisms and topics, today's studies call for a stronger focus on specific components of a question in the hopes of answering one great question even through a couple of small answers. In this thesis, I therefore apply the abovementioned concepts in answering three specific questions and, in doing so, hope to contribute in the understanding of: What determines species diversity?

In **Chapter 1** I focus on the difference between local (small scale) and regional (large scale) patterns of species diversity. I use the species area relationship to answer the question: **Does area link regional to local diversity along elevational gradients**? I calculate the degree to which differences between local and regional elevational species richness patterns can be accounted for by the effects of regional area. I use five elevational transects (in Costa Rica, Ecuador, La Réunion, Mexico, and Tanzania) which have been sampled for fern diversity in standardized field plots and collated in regional species lists based on herbarium and literature data. I then used the Arrhenius function $S = cA^z$ to correct regional species richness for the effect of area using three slightly different approaches, and compared the concordance of local and regional patterns prior to and after accounting for the effect of area on regional richness using linear regression analyses. I found a better concordance between local and regional elevational species richness after including the effect of area in the majority of cases. In several cases, local and regional patterns were very similar after accounting for area. In most of the cases, the maximum regional richness shifted to a higher elevation after accounting for area. Different approaches to correct for area resulted in qualitatively similar results. Therefore I conclude that differences between local and regional elevational richness patterns can at least partly be accounted for by area effects,

suggesting that the underlying causes of elevational richness patterns might be the same at both spatial scales.

This chapter significantly contributes to the question "What drives species diversity?" by showing that area is important in linking species diversity from regional to local scale and that regional diversity can be "corrected" using regional area.

In **Chapter 2** I investigate the effect of the regional (large scale) species pool on local (small scale) community composition. I use an island size gradient with variation in species pool sizes from small to large pools to answer the question: **In what way does the regional species pool and local environmental heterogeneity influence local community composition (β diversity) and how are these two aspects linked?** Using a hypothesis-driven approach, I disentangle the species pool from environmental heterogeneity by separately studying local β diversity of ferns within islands as well as along an island size gradient with increasing species pool sizes. I find that along the island size gradient, β diversity is driven by the species pool, while within islands, it is driven by environmental heterogeneity. In addition, the explanatory power of environmental heterogeneity depends strongly on the species pool. Using niche overlap between species as well as species abundance based approaches, I show that increasing competition at sites with large species pools provides a biotic explanation for how the species pool influences local β diversity.

This chapter considerably contributes to the question "What drives species diversity" by providing a simple, elegant, and empirical model of how the species pool drives local community composition.

In **Chapter 3** I investigate **whether the equilibrium theory of island biogeography is equally applicable at regional and local spatial scales** and if the echo pattern influences local diversity equally across a range of sampling scales. I use 12 mountain regions on islands of different sizes, isolation, and environmental conditions in Indonesia and the Philippines. I sampled ferns in standardized field plots in a fixed spatial design at seven different spatial scales (plot to island). I then used the two main components of the theory of island biogeography—area and isolation—in combination with local and regional environmental factors to test their predictive power on diversity at the different scales using ordinary least square regression and relative variable importance. I found that the equilibrium model of MACARTHUR and WILSON applied best at regional scales. The explanatory power of area increased with spatial scale except at the most local scale. The strength of the negative relationships among diversity and isolation decreased with increasing spatial scale. We found evidence for an echo pattern at large to intermediate but not at small spatial scales. Based on these observations I conclude that the two main components of the theory of island biogeography—area and isolations—are good predictors of biodiversity at regional scales. The species pool has a scale dependent influence on diversity and is unimportant at the local scale where environmental conditions are better predictors of diversity. To make predictions about diversity on islands it is therefore important to take the scale dependence of the echo pattern into account.

This chapter effectively contributes to the question "What drives species diversity" by showing that the equilibrium theory of island biogeography does not apply at all spatial scales, explaining it using the influence of a spatially scaled echo pattern.

Chapter 4 diverts from the pursuit of "What drives species diversity" and, rather, tries to solve a practical problem many researchers have while working in the tropics. To investigate the drivers of species diversity, we have to somehow collect data on the relevant environmental parameters. This is easy for some parameters. But for others—like precipitation, productivity, and temperature—global models exist nowadays; other parameters like soil fertility and relative humidity cannot be easily derived from such models. Collecting soil samples is rather unproblematic in this regard, since this can be done while accessing local species diversity. The problematic factor is relative air humidity. Being a crucial environmental factor for influencing the physiology of many organisms, ignoring it in an analysis on species diversity might lead to wrong conclusions. It is, however, logistically challenging to measure it in remote environments over a long period, since it requires at least visiting a sampling site twice. For some of the remote mountains sampled for this thesis there are significant financial and logistical differences (Chapter 2 would have needed 30 instead of 15 expeditions to remote mountains on even more remote islands). To solve this problem, relative humidity was measured in all mountains in the Philippines for at least one year and the data was pooled together with data from Costa Rica and Ecuador to **evaluate if visually accessed bryophyte cover on trees was a viable proxy for relative air humidity**. Several authors had already suggested bryophyte cover as proxy for relative air humidity, but a quantitative study on the matter was still lacking. Therefore I compared microclimatic measurements of air humidity with epiphytic bryophyte cover at 26 study sites in tropical forests where microclimate has been measured for at least 12 months. Across all sites, bryophyte cover was, however, weakly related to relative air humidity; but when we separated highland (1800–3500 m elevation) from lowland (<1800 m) sites, relative air humidity showed significant and distinct relations to bryophyte cover. I conclude that epiphytic bryophyte cover can be used as a proxy for air humidity if temperature and elevation are taken into account within a circumscribed study region, but might not be applicable for comparisons across extensive elevational gradients or wide differences in temperature.

Aside from Chapter 4, which deals with bryophytes, the model organism group I work with are ferns. I first got in touch with ferns by sketching them for the "*Forthcoming Guide to the Ferns of Bolivia*" in my first year of studies in Göttingen. Hugely fascinated by them, I realized their enormous potential for species diversity studies inspired by the work of MICHAEL KESSLER, HANNA TUOMISTO and KALLE RUOKOLAINEN, who all used them as model organisms. Ferns have characteristics that make them a perfect model organism for biodiversity studies:

- they are distributed worldwide with 10,000-12,000 described species
- they have a high diversity in tropical mountains
- they are the main contributors to the terrestrial herb flora
- some fern lineages belong to the most species rich epiphytic plant groups in tropical mountains (e.g. Gentry 1990).

Ferns comprise distinct ecological guilds and are independent of biotic pollination and distribution vectors because of their spore dispersal (Barrington 1993). Their high diversity allows statistical inference of the documented data, and the relatively lower dependence from biotic vectors allows one to link patterns of distribution directly to abiotic factors. But perhaps most importantly, they don't run away when you try to catch them.

I hope this thesis impacts biodiversity research and biogeography by answering some important questions that bring us closer to answering the overall question: "What determines

species diversity?" I hope that the effects that spatial scale has on the perception of species diversity will be incorporated in more studies, despite their difficulties and challenges. I also hope I am able to provide anyone who reads this thesis some valuable insight on how species diversity is influenced by spatial scale and, on a loftier note, able to inspire further scientific research in this field: there are still myriad unanswered questions out there that lie in wait, that summon, that provoke...that push us ever forth the boundlessness of discovery.

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View from 1100 m elevation across the lowlands of the island of Seram in Indonesia.

Morning in the central highlands of Buru, Indonesia.

View from the island of Bacan in Indonesia northwards, taken during the climb of Mt. Sibela.


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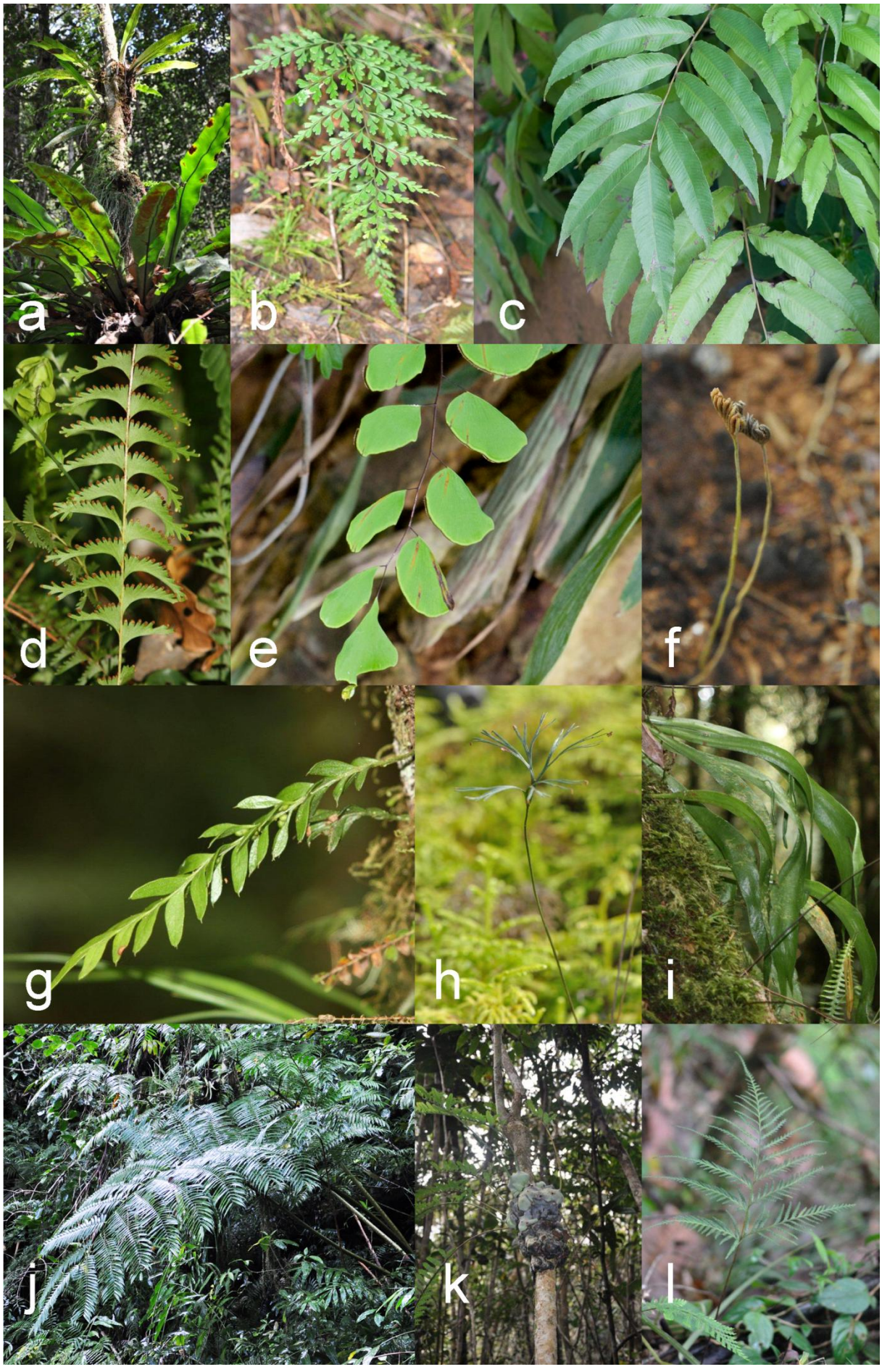
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Previous pages:

Page 18: Impressions of the cloud forests of the malesian archipelago in which the sampling plots got established (Capter 2 – 4): (a) Mt. Kitanglad, Mindanao, Philippines. (b) Seram, Malukku, Indonesia. (c) Arfak Mountains, New Guinea, Indonesia.

Page 19: Some examples for the enormous amount of fern diversity in the cloud forests of Indonesia and the Philippines: (a) *Asplenium nidus* growing epiphytic in the Mingan Mountains of Luzon, Philippines. (b) *Lindsaea bouillodii* a terrestrial fern of the growing on the ultramafic soils of Mt. Hamiguitan, Mindanao, Philippines. (c) *Pronephrium rohmbeum*, cultivated specimen in the fernery of the Central Mindanao University. (b) *Lindsaea apoensis*, growing at Mt. Kitanglad, Mindanao, Philippines. (e) *Adiantum philippinensis*, an endemic fern from the Philippines, cultivated specimen in the fernery of the Central Mindanao University. (f) *Schizaea digitata*, a small, grasslike fern growing on the slopes of Mt. Hamiguitan, Mindanao, Philippines. (g) *Tmesipteris lanceolata*, a fern ally growing on a treefern trunk at Mt. Kitanglad, Mindanao, Philippines. (h) *Schizaea dichotoma*, growing on the ultramafic soil of Buru, Indonesia. (i) *Ophioglossum pendulum*, an epiphytic fern growing throughout the Malesian Archipelago, this picture was taken in Seram, Indonesia. (j) *Angiopteris palmiformis*, one of the biggest fern species with up to 5 meter long fronds, from Panay, Philippines. (k) *Leconopteris deparioides*, an ant fern, the bulbous structure is the hollow rhizome of the fern which gives shelter to certain ant species. Mt. Hamiguitan, Philippines. (l) *Tarpeinidium calomelanos* growing in the Mingan Mountains of Luzon, Philippines.

Chapter 1

The effect of area on local and regional elevational patterns of species richness

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ORIGINAL ARTICLE

The effect of area on local and regional elevational patterns of species richness

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ABSTRACT

Aim To calculate the degree to which differences between local and regional elevational species richness patterns can be accounted for by the effects of regional area.

Location Five elevational transects in Costa Rica, Ecuador, La Réunion, Mexico and Tanzania.

Methods We sampled ferns in standardized field plots and collated regional species lists based on herbarium and literature data. We then used the Arrhenius function $S = cA^z$ to correct regional species richness (S) for the effect of area (A) using three slightly different approaches, and compared the concordance of local and regional patterns prior to and after accounting for the effect of area on regional richness using linear regression analyses.

Results We found a better concordance between local and regional elevational species richness after including the effect of area in the majority of cases. In several cases, local and regional patterns are very similar after accounting for area. In most of the cases, the maximum regional richness shifted to a higher elevation after accounting for area. Different approaches to correct for area resulted in qualitatively similar results.

Main conclusions The differences between local and regional elevational richness patterns can at least partly be accounted for by area effects, suggesting that the underlying causes of elevational richness patterns might be the same at both spatial scales. Values used to account for the effect of area differ among the different study locations, showing that there is no generally applicable elevational species–area relationship.

Keywords
Altitude, diversity, ferns, local diversity, pteridophytes, regional diversity, species–area relationship, tropical mountains.

INTRODUCTION

Understanding the factors that drive gradients of species richness is one of the major challenges of ecological and biogeographical research. Regressing patterns of species richness against sets of variables that are presumed to be potentially responsible for these patterns is a common method, and comparing results from many studies enhances our insight into the nature of the distribution of species richness. The crucial problem is that comparing results from different studies requires comparable methods of data collection, especially concerning the basic data source. Studies documenting patterns of species richness can be divided into two main groups (Romdal & Grytnes, 2007). The first focuses on field inventories in a specific area (hereafter: local studies), whereas the second derives its data mainly from literature and scientific collections (hereafter: regional studies). These approaches differ substantially in geographical extent and data quality as well as in the factors that influence them (Fig. 1).

Neither of the two approaches can a priori be said to be superior to the other, because both have their own advantages and drawbacks. In general, local studies are costly, time-consuming and typically cover just a minute portion of the surface area, as well as only part of the regional biota, especially

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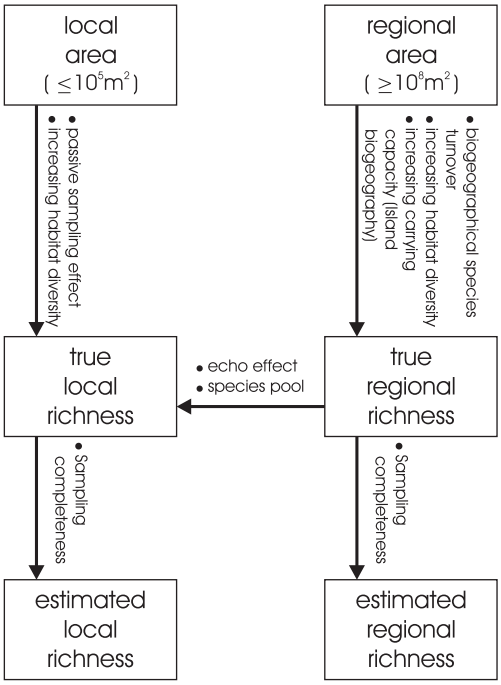

Figure 1 Factors linking local and regional species richness to area. The true local and the true regional richness are the actual values of a given area. Because every sampling method has its own specific error and will not sample the complete richness (sampling completeness), it is impossible to measure this value exactly. Because of this, every method applied always results in an estimate of species richness (estimated local and regional richness). Area influences true richness in a number of ways, depending on the scale of the area. For the local area, the representativeness of small plots (which increases as plot size increases: passive sampling) and small-scale changes of habitats are the main factors influencing true local richness. At the regional scale, effects of biogeographical species turnover, increasing large-scale habitat diversity, and increasing carrying capacity have to be taken into account. True regional richness influences true local richness by providing the species pool from which true local richness is recruited. The abundance of species within this species pool increases with the size of the regional area and affects local richness by the higher dispersal probability into the local area (echo effect). We defined local and regional area at the spatial scales typically found in ecological studies, leaving a gap between them that is typically too large for plot sampling and too small for regional studies.

in species-rich environments (Whitmore *et al.*, 1985). Thus, a constant sampling intensity in different environments may result in a systematic undersampling in species-rich communities compared with species-poor communities (Lawton *et al.*, 1998). Properly conducted local studies have the advantage of a standardized sampling method, thus eliminating the influence of varying sampling intensity and sampling area on observed richness patterns. A further problem of local studies is that ongoing habitat destruction makes it increasingly difficult to find natural habitats for sampling.

Regional studies, on the other hand, are advantageous because richness patterns can be studied without costly field surveys by data mining based on extensive prior studies, which often include areas that can no longer be sampled because of habitat destruction. Regional studies cover larger areas and larger fractions of the total biota because they combine data from numerous collecting efforts. Collectors, however, usually prefer easily accessible areas that look particularly interesting, so field collections tend to be spatially uneven (Nelson *et al.*, 1990; Soria-Auza & Kessler, 2008). They might also focus on rare and interesting species, such that common species are under-represented. Actual species records are always patchy and it is contentious whether species distributions should be interpolated between records. Along elevational gradients, for example, some authors have suggested that species should be considered as present in a given elevational belt if they have been recorded at both higher and lower elevations (Williams *et al.*, 1996; Lees *et al.*, 1999). This may, however, cause artificially elevated species numbers at mid-elevations, because such interpolated data are overproportionally added to mid-elevations as opposed to edges of the gradient (Grytnes & Vetaas, 2002). Moreover, unusual distribution patterns (e.g. bimodal) may be masked (Hemp, 2002).

Patterns of species richness along elevational gradients have received considerable attention in the last decade, and have become firmly established as a complementary, replicable alternative to the traditional studies of latitudinal gradients (Rahbek, 1995, 2005; Lomolino, 2001). At both the local and regional level, elevational richness patterns across a wide range of taxa commonly show a more or less hump-shaped pattern, with maximum richness at some intermediate point of the gradient (Rahbek, 1995, 2005; Grytnes & McCain, 2007). Such patterns have been documented for mammals (McCain, 2005, 2007), birds (Herzog *et al.*, 2005; McCain, 2009), reptiles (Fu *et al.*, 2006), moths (Brehm *et al.*, 2007), flowering plants (Hemp, 2001; Moser *et al.*, 2005; Oommen & Shanker, 2005), vascular epiphytes (Küper *et al.*, 2004; Krömer *et al.*, 2005; Cardelús *et al.*, 2006; Hemp, 2011), ferns (Hemp, 2001; Bhattarai *et al.*, 2004; Carpenter, 2005; Kluge *et al.*, 2006) and bryophytes (Grau *et al.*, 2007). In addition, some studies have revealed monotonic declines of species richness from lowlands to high elevations (e.g. Araceae: Kessler, 2002; Acebey & Krömer, 2008), or roughly constant values from lowlands to mid-elevations, followed by a marked decline (Rahbek, 1995, 2005; Kessler, 2001). The causes determining elevational patterns of species richness are still being debated, but include the combined effects of surface area, geographical constraints, climate and ecosystem productivity, evolutionary and historical processes, and population-level processes such as source–sink effects (Grytnes & McCain, 2007; McCain, 2009). The degree to which these causes may differently influence local and regional patterns remains unclear.

The studies listed above include both local and regional approaches. Biases of both types of studies may be expected to result in different perceptions of patterns of species richness (Kessler *et al.*, 2009). It is still unknown if local and regional studies differ in any systematic way, and hence it is unclear whether they can be combined, for example in meta-analyses

of elevational richness patterns (McCain, 2009). In a recent comparison of elevational richness patterns recovered from local and regional studies, Kessler *et al.* (2009) found minor, but distinct, deviations between the two approaches. This might be a result of statistical noise, but there may also be a systematic deviation between the two types of datasets.

Kessler *et al.* (2009) suggested that regional area may lead to deviations between local and regional richness, as area is well known to influence patterns of species richness through a variety of mechanisms at various scales (Rosenzweig, 1995). At a regional scale, larger areas are well known to support more species, both because they maintain viable populations of more species and because they typically include higher habitat diversity (MacArthur & Wilson, 1967; Drakare *et al.*, 2006). As land surface area typically declines with increasing elevation (Körner, 2000; Lomolino, 2001), regional species richness may be expected to peak at lower elevations compared with local richness. For this reason, a number of studies have corrected the regional number of species along elevational gradients for area effects (e.g. Rahbek, 1997; Sanders, 2002; Bachman *et al.*, 2004).

At the local scale, larger sampling areas typically include more species because they more completely sample the regional species pool ('passive-sampling hypothesis', Connor & McCoy, 1979). However, even if sampling area is held constant, regional area will influence local species indirectly through the increase of the regional species pool ('echo-effect', *sensu* Rosenzweig & Ziv, 1999; see also Brehm *et al.*, 2003; Herzog *et al.*, 2005). This indirect effect of regional area on local species richness has been documented in a meta-analysis including 71 published local elevational transect datasets (Romdal & Grytnes, 2007). This analysis, however, was based only on correlation analyses between local richness and regional area, without considering possible co-variances of other factors. For example, if local species richness is influenced by climatic factors that systematically change with elevation (e.g. temperature), and regional area also changes systematically with elevation, then a spurious correlation between local richness and regional area may result. To unravel any causal relationships between local richness and regional area, it is thus necessary to consider the intermediate link between them, that is, regional richness.

In this study we therefore extend the approach of Romdal & Grytnes (2007) by taking regional richness into account. Because the proposed indirect effect of regional area on local richness is mediated through regional richness, consideration of the latter can help to discern the causality of these relationships more clearly.

To test this assumption, we compiled data from both local and regional studies of ferns and lycophytes (hereafter collectively termed simply ferns) along five elevational gradients (Pichincha in Ecuador, Braulio Carrillo in Costa Rica, Los Tuxtlas in Mexico, Kilimanjaro in Tanzania, and La Réunion). Our aim was to assess the difference in local and regional patterns, and to calculate the degree to which these differences can be accounted for by the effects of area.

MATERIALS AND METHODS

Local elevational species richness data were derived from five field studies using the same consistent sampling method (except for the Kilimanjaro transect, where the plot area was 1000 m^2) (Table 1 and Appendix S1 in the Supporting Information). Sample plots of 400 m^2 each, and of square shape, were placed in natural forest, that is, avoiding secondary vegetation and special habitats such as gaps, ravines or ridges, in order to keep vegetation structure as homogeneous as possible (Kessler & Bach, 1999; Kessler, 2001). Local species richness is given by the mean number of species in all plots sampled in a given elevational band. Regional richness data were generated from published databases and species lists (Table 1). Elevational extremes for each species in the study regions were interpolated to generate distribution data of species for each elevational belt under the assumption that species have continuous distributions (Grytnes & Vetaas, 2002). We defined regional area as the land surface covering the respective elevational belt where the regional richness data were obtained. For example, the regional area for the La Réunion transect consisted of the surface area of the whole island, because only specimens collected on this island were

Table 1 Data type and sources of the five local and regional datasets of elevational fern and lycophyte species richness. For the regional data, in some cases richness estimates were corrected by interpolation of elevational species ranges between the recorded elevational maxima. The number of sample plots per elevational belt is provided in Appendix S1.

Transect	Scale	Method	Source	Data correction
Pichincha	Local	22 plots of 20 × 20 m	M. Kessler & M. Lehnert, unpublished data	No
	Regional	Country list	Jørgensen & León-Yánez (1999)	
Costa Rica	Local	156 plots of 20 × 20 m	Kluge *et al.* (2006)	Interpolation
	Regional	Regional flora	Moran & Riba (1995)	
Los Tuxtlas	Local	42 plots of 20 × 20 m	T. Krömer & A. Acebey, unpublished data	No
	Regional	Country flora	Mickel & Smith (2004)	
Kilimanjaro (south side)	Local	379 plots of 1000 m^2	Hemp (2001)	Interpolation
	Regional	Regional list	Hemp (2002)	
La Réunion	Local	29 plots of 20 × 20 m	M. Kessler, unpublished data	No
	Regional	Herbarium records	M. Kessler, unpublished data	

used to calculate the regional species richness. Surface area was calculated for Los Tuxtlas, Kilimanjaro, La Réunion and Pichincha using Spatial Analyst in ArcView 3.2 (ESRI, Redlands, CA, USA). For the Costa Rica transect, we estimated the proportion of total area found at intervals of 100 m in a 30-km-wide strip in Braulio Carrillo National Park and on Cerro de la Muerte (local transect area) by counting grid cells on topographical maps (1:50,000) between the contour lines (Kluge *et al.*, 2006).

Our assessment of the mismatch between local and regional richness patterns by incorporating the effect of regional area was based on the Arrhenius (1921) equation,

$$S = cA^z, \quad (1)$$

where S is the number of species, c is the number of species in the smallest sampling area, A is area (in arbitrary units), and z is a constant describing the slope of the species–area relationship in the log–log space.

In our case, we set S = observed regional species richness, and c = theoretical (area-corrected) regional richness at an arbitrary minimum area common to all elevational belts. This resulted in the formula:

$$S_R = S_{Rcor}A^z, \quad (2)$$

where the subscript 'R' indicates regional species richness and the subscript 'cor' indicates area-corrected values. To calculate S_{Rcor}, this equation was then modified to

$$S_{Rcor} = S_R/A^z. \quad (3)$$

The main challenge of applying this formula was to obtain realistic z-values in the Arrehnius function. These values can be derived empirically from the slope of the species–area relationship in log–log space. Deriving the z-value by using the slope of a species accumulation curve is difficult in this case, because our small dataset shows a high degree of variance. In addition, z-values can vary with spatial scale (Crawley & Harral, 2001), and basing our estimates on just one single derived z-value might be misleading. Thus we used two additional approaches to estimate the z-value and validate the results of the empirically derived z-values. The second approach consisted of a nonlinear model ($S_R = S_LA^z$) to estimate the z-value that will give the best concordance between regional species richness (S_R) and local species richness (S_L) patterns. The calculated z-values from the nonlinear model were then used to correct for the effect of area, and the resulting patterns of corrected regional richness were then compared with local richness using linear regression analyses. Because empirical z-values typically fall between 0.2 and 0.4 and cannot be higher than 1 or lower than 0 (MacArthur & Wilson, 1967; Rosenzweig, 1995; Crawley & Harral, 2001), we used a range from 0 to 1 for z in the model. Our third approach used linear regression analyses between local and regional richness. We checked the values of the coefficient of determination (R^2) given by the linear regression between local and regional richness for all z-values ranging from 0 to 1 in steps of 0.01. To test if a linear regression is valid to describe the relationship between local and regional richness, we calculated Akaike's information criterion (AIC; Wagenmakers, 2004) using a linear and a quadratic nonlinear model. Because the number of observations divided by number of parameters sometimes falls below 40 (for the small datasets: Pichincha, La Réunion, Los Tuxtlas), we used the bias-corrected form, AIC_c (Burnham & Anderson, 2002).

Prior to the analyses, we transformed species numbers and area at each elevational band relative to a maximum of 100 to eliminate the effects of different measuring units as well as to make the patterns graphically more easily comparable. Trend lines within the figures were fitted with distance-weighted least-squares smoothing, using Xact 7.2 (SciLab, Hamburg, Germany).

Finally, we compared the elevational patterns of local richness with uncorrected and area-corrected regional species richness through linear regression analyses. All calculations were carried out in spss 11.5 and R (R Development Core Team, 2008).

RESULTS

Values of the coefficient of determination (hereafter: regression values) of the linear regression analyses between local and uncorrected regional species richness ranged from 0.24 (Kilimanjaro) to 0.84 (La Réunion) (Table 2). On four transects (Costa Rica, Kilimanjaro, La Réunion, Los Tuxtlas), uncorrected regional species richness peaked at a lower elevation than did local richness, whereas along the Pichincha transect, peaks roughly coincided in elevation (Fig. 2).

After accounting for the effect of area, regional richness peaks shifted upwards (Fig. 2), resulting in higher regression values with local richness along all transects (Table 2). Using the empirically derived z-values, regression values increased to 0.58 (Kilimanjaro), 0.79 (Costa Rica), 0.88 (La Réunion) and 0.89 (Pichincha) and decreased for Los Tuxtlas.

When we used the z-values obtained by estimation of the z-value using the nonlinear model, regression values increased to 0.53 (Los Tuxtlas), 0.88 (Pichincha and La Réunion), 0.72 (Costa Rica) and 0.55 (Kilimanjaro).

The test for all possible z-values from 0 to 1 showed higher regression values between local and regional richness for small z-values ($z < 0.45$) for Kilimanjaro, Costa Rica, Pichincha and La Réunion. For Los Tuxtlas, higher regression values between local and regional richness were obtained at z-values < 0.26. When we used the z-values that resulted in the highest concordance of local and regional richness, regression values were, unsurprisingly, higher. In one case (Los Tuxtlas) the regression values were considerably higher than those obtained with the empirically derived z-value and the z-values estimated by the nonlinear model, whereas in the other cases they reached similar values. Interestingly, derived z-values of all three approaches were often in good concordance (standard deviation: $z \pm 0.1$). Thus, at Kilimanjaro, the empirically estimated z-value was 0.63, while the highest regression value was obtained with a z-value of 0.69, and the nonlinear model

Table 2 Empirically derived *z*-values, *z*-values estimated with the nonlinear model (nlm), and *z*-values that resulted in the highest concordance between local and regional richness. Linear regressions were calculated for local richness versus uncorrected regional richness, as well as against regional richness corrected with the empirically derived *z*-values, the derived *z*-value from the nonlinear model (nlm), and the *z*-value calculated with the linear model that resulted in the highest regression values between local and regional richness (highest R^2).

	z-values			R^2-values			
				Regional richness corrected for area with *z*-values derived by:			
Transect	Empirical	nlm	Highest R^2	Uncorrected	Empirical	nlm	Highest R^2
Kilimanjaro	0.63	0.53	0.69***	0.24**	0.58***	0.55**	0.59***
Costa Rica	0.26	0.11*	0.27***	0.60***	0.79***	0.72**	0.79***
Los Tuxtlas	−0.05	0.21	0.06**	0.36*	0.30	0.53*	0.75**
La Réunion	0.16	0.21	0.36***	0.84***	0.88***	0.88**	0.89***
Pichincha	0.27	0.26	0.19**	0.79**	0.89**	0.89**	0.89**

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

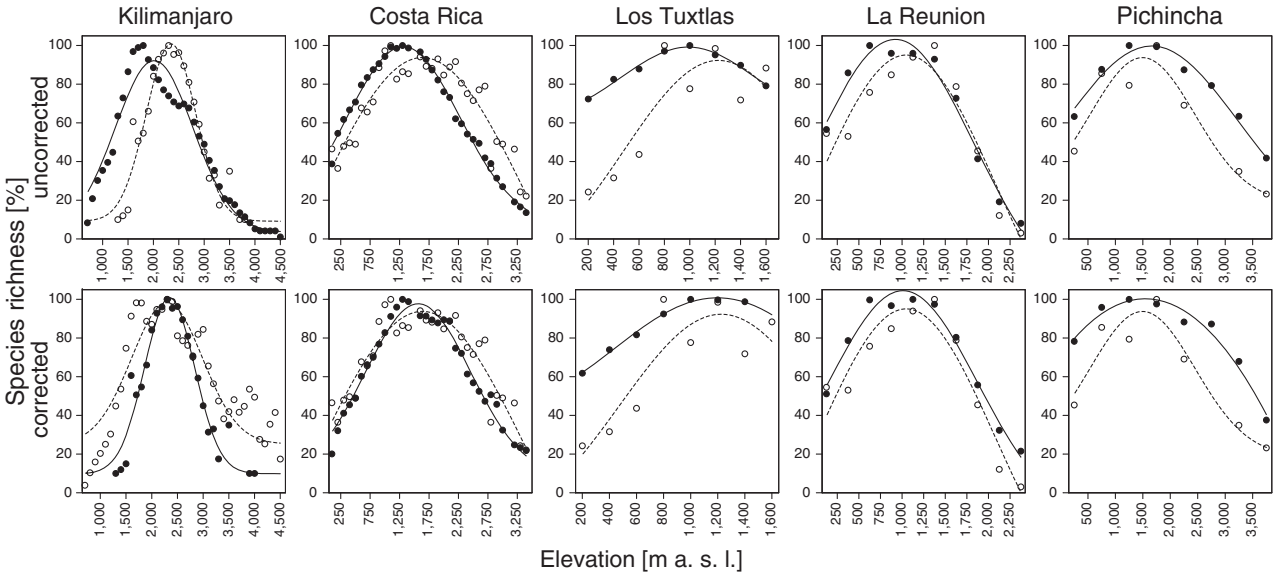

Figure 2 Uncorrected and area-corrected patterns of regional (black circles, continuous lines) and local (open circles, dashed lines) fern and lycophyte species richness along all five elevational transects. To account for the effect of area, the following *z*-values were used: Costa Rica = 0.27; Kilimanjaro = 0.69; Pichincha = 0.19; La Réunion = 0.36; Los Tuxtlas = 0.6. Trend lines were fitted with distance-weighted least-squares smoothing, using Xact 7.2 (SciLab, Hamburg, Germany). Note that species numbers for each elevation were transformed to a relative maximum of 100 prior to analysis to make elevational trends visually comparable.

predicted a *z*-value of 0.53. Similar deviations were found at all other sites. The AIC_c values for the linear model were lower than those for the non-linear model for all sites when testing the relationship between local and regional richness. Differences of the AIC_c values ranged from 8.4 in Los Tuxtlas to 1.45 at Kilimanjaro.

DISCUSSION

Our results support the assumption that area is partly responsible for the observed differences between local and regional species richness patterns along elevational gradients. Often, local and regional species richness patterns along such transects are already in good concordance (Herzog *et al.*, 2005; Kessler *et al.*, 2009), as best shown in our dataset by the Pinchinca and La Réunion transects (Fig. 2). However, both in our study and more generally, regional richness patterns tend to show peaks at lower elevations compared with local species richness (Kessler *et al.*, 2009). By statistically accounting for the effect of varying surface area along the study gradients on the estimates of regional species richness, as previously applied for example by Rahbek (1997), Sanders (2002) and Bachman *et al.* (2004), we improved the concordance between local and regional richness patterns. In several cases, especially in Costa Rica, La Réunion

and Kilimanjaro, local and regional patterns were very similar after accounting for area (Fig. 2). In all cases, the maximum regional richness shifted to a higher elevation after accounting for area, so that regional area seems to be the main factor responsible for these deviations in maximum species richness. This strongly implies that, despite the indirect character of the area effect on local richness (Rosenzweig & Ziv, 1999; Romdal & Grytnes, 2007), regional richness is influenced to a greater degree by area than is local richness. This difference is intuitively appealing, considering that local richness is clearly spatially restricted and depends on the size of the local sampling units. Thus, richness in smaller units may be primarily limited by the number of individuals and hence species that fit into small areas (Romdal & Grytnes, 2007). Indeed, Romdal & Grytnes (2007) found that the indirect area effect increased with increasing sample size in their meta-analysis. As we used only two sizes of sample plots (400 m^2 on most transects, 1000 m^2 on Kilimanjaro), we are unable to conduct a similar analysis. It would be worthwhile, however, to apply our approach to transect datasets where local richness has been sampled at different scales, such as the Norwegian dataset of Grytnes (2003).

Although we used the species–area relationship to account for the area effect on regional area, this does not imply that we consider that we cannot account for the effect of regional area on local richness estimates. Our aim was to assess the degree to which the different effects of regional area on local and regional richness estimates lead to the observed differences in elevational richness patterns. We could just as well have conducted the analysis the other way around, accounting for area on local richness to match regional richness. Indeed, we did such an analysis, but because it produced qualitatively identical results, the results are not reported here.

Accounting for area effects did not result in perfect concordance between local and regional richness, and concordance was higher at three localities (Kilimanjaro, Costa Rica, Los Tuxtlas) than at the other two. Especially for the three transects with R^2 values > 0.8, the remaining variance may simply reflect sampling noise. In other cases, however, especially where local and regional patterns remain distinctly different despite accounting for area and where regression values remain relatively low, additional factors may play a role. Another potential reason for the continuing mismatch between local and regional richness estimates despite taking regional area into account is that, in mountains, ground surface area is also influenced by the inclination of the mountain slopes and the roughness of the terrain, so that steeper and more dissected mountains have a larger total area (Vetaas & Grytnes, 2002; Rahbek *et al.*, 2007). We did not attempt to model this effect for two reasons. First, estimates of the three-dimensional surface area depend on the spatial resolution of the digital elevation models, making it difficult to choose a 'correct' one. Second, plants still grow upright on mountain slopes, so that a higher three-dimensional surface area does not necessarily lead to proportional changes in the number of plant individuals. At the same time, very steep slopes may not be inhabited at all by most plants, despite their large surface area. One remaining reason for the continuing mismatch between local and regional richness patterns could be the different data corrections that we used for the regional richness (Table 1). These data corrections, however, only accounted for minor differences in the magnitude of statistical noise between the patterns, and therefore were not taken into account.

Along three of our study transects (Kilimanjaro, Los Tuxtlas, La Réunion), regional area estimates accounted for the entire mountain or mountain range. On the remaining transects (Costa Rica, Pichincha), regional area was delimited in a more arbitrary way to include the ecologically homogeneous regions about 100–200 km north and south of the study transects. This approach was also influenced by the availability of regional distributional data, which are often given only for large political entities, for example the country Costa Rica, forcing us to accept these entities as regions. This certainly affected our estimates of both regional area and regional species richness, but we do not consider that this fundamentally influenced our analyses because both parameters were evaluated for the same region. Had we chosen a larger regional area, then regional richness estimates would also have increased. While the absolute values of the relationships between local and regional richness would then also change, the qualitative relationships between local and regional richness estimates would be maintained.

The best concordance of local and regional richness after accounting for area effects was achieved with different *z*-values

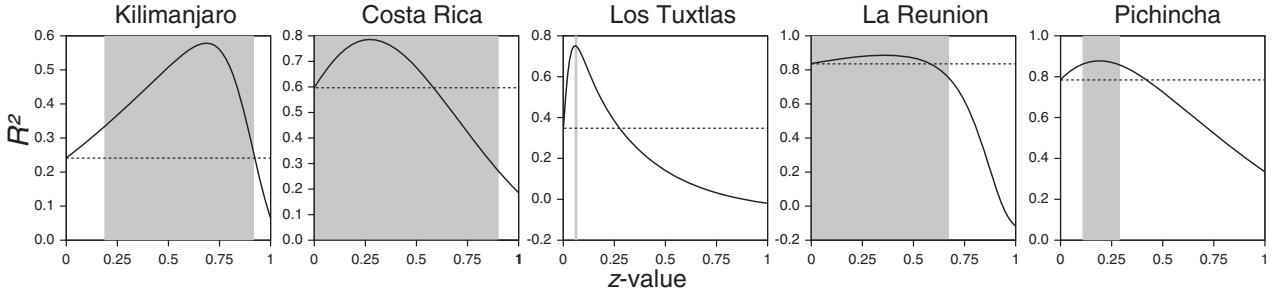

Figure 3 *z*-values ranging from 0 to 1 and the resulting regression values between local and regional richness patterns of ferns and lycophytes when the respective *z*-values are used to correct for area. The continuous bold lines show the R^2 values for 100 steps of *z*-values (0, 0.01, 0.02, etc.). The dotted lines indicate the R^2 values of the uncorrected richness patterns. The grey area indicates where regression values are highly significant ($P \leq 0.001$).

on each of the five study transects. This underlines the observation that *z*-values are not a given constant but rather are dynamic and hard to estimate (Crawley & Harral, 2001). Our three approaches for estimating *z*-values arrived at qualitatively similar but quantitatively different results. The derived *z*-values using the three approaches in many cases differed to some degree from each other. However, all of the three approaches have their strengths and weaknesses. Empirically derived *z*-values are the only ones that can be directly derived from the data and might therefore be the best choice. However, for small datasets with only a few data points, there is a relatively high probability that the derived *z*-value might be inaccurate. This might be the case for Los Tuxtlas, where the empirical *z*-value is actually negative.

Calculating regression values with all possible *z*-values shows that better concordance of local and regional richness can be achieved when using *z*-values < 0.45 for most localities (Fig. 3). *z*-values in this range have been also reported in previous studies (MacArthur & Wilson, 1967; Rosenzweig, 1995; Crawley & Harral, 2001), while higher *z*-values, which in our study lead to lower concordance between local and regional richness, are rarely documented. This approach helps in finding the *z*-value that results in the highest concordance between local and regional richness, but it may not result in empirically realistic values.

The values estimated with the nonlinear model take into account that local–regional richness relationships can be nonlinear. On the other hand, the AIC_c values calculated to test for a linear versus a nonlinear relationship between local and regional richness show that a linear model is probably more appropriate. However, the good qualitative concordance of the *z*-values for all models (with some deviations for Los Tuxtlas) and the qualitatively similar results in most of the cases, irrespective of the approach used to select the *z*-values, support the conclusion that differences between local and regional elevational richness patterns can partly be accounted for by the effect of area on regional richness.

At present, we are unable to explain the causes of the different local versus regional patterns. They could be the result of uneven or incomplete regional sampling. They might, however, also reflect the fact that local sampling was usually restricted to forest habitats whereas regional species lists included species from a wider range of habitats, although these habitats typically have fewer fern species (Hemp, 2001; Kessler, 2001). Finally, these differences may reflect spatially varying impacts of factors that influence elevational richness patterns, such as temperature and humidity (Bhattarai *et al.*, 2004; Krömer *et al.*, 2005; Kluge *et al.*, 2006), as well as energy availability and ecosystem productivity (Hawkins *et al.*, 2003; Currie *et al.*, 2004), historical and evolutionary processes (Ricklefs, 2004; Wiens & Donoghue, 2004; Smith *et al.*, 2007), source–sink effects (Grytnes *et al.*, 2008; Kessler, 2009), or even human impact (Nogués-Bravo *et al.*, 2008; Marini *et al.*, 2010).

In conclusion, regional surface area seems to be largely responsible for the differences between local and regional species richness patterns along elevational gradients. This has important implications for studying and understanding elevational diversity patterns. First, from an analytical point of view, we suggest that a direct comparison of local and regional patterns is feasible once the latter have been corrected for area effects. This may greatly increase the number of studies that can be combined in meta-analyses (e.g. McCain, 2009). More fundamentally, if area is indeed the only factor important for the difference between local and regional elevational richness patterns, then the similarity between the two patterns may be taken as an indication that both are reflections of one general pattern driven by a common suite of underlying processes, rather than by different processes at different spatial scales.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Number of sampled plots per location.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCHES

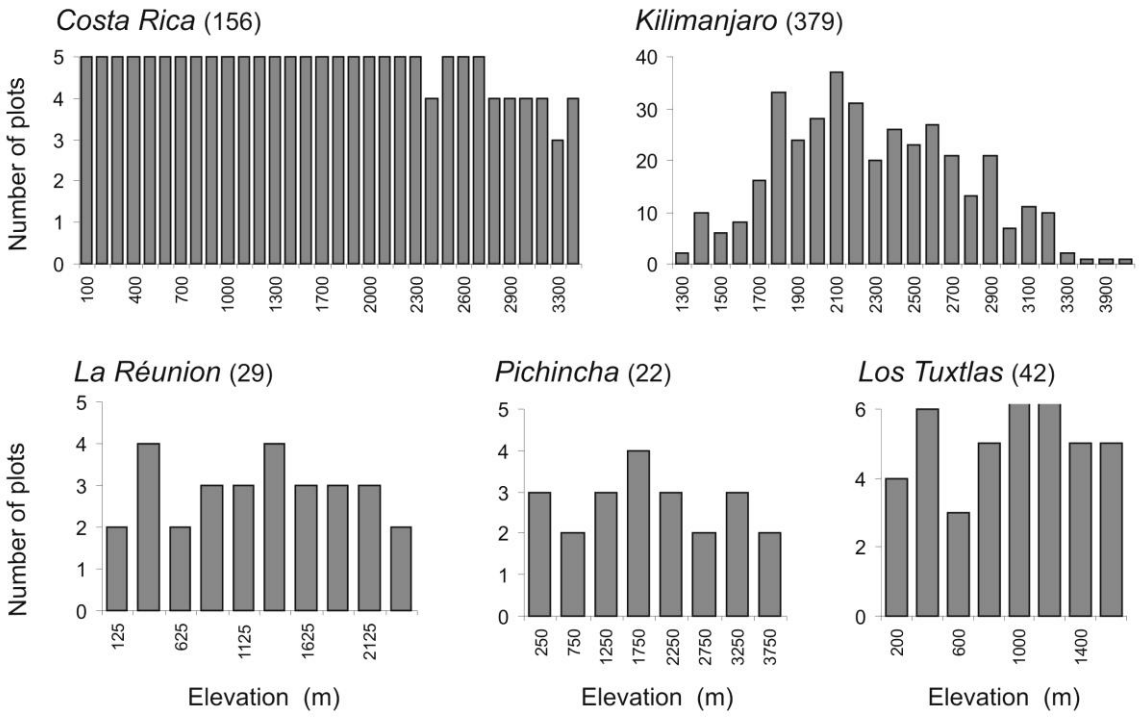
Dirk N. Karger is a PhD student at the Department of Systematic Botany at the University of Zurich, Switzerland. His current research focuses on patterns of diversity among ferns on islands of different sizes in the Philippines and Indonesia.

The authors share a strong research focus on tropical montane forests, including ferns. Together, they are interested in understanding how tropical mountain biodiversity has evolved and is maintained, and how it can be sustainably managed.

Author contributions: D.K., J.K. and M.K. conceived the ideas; J.K., T.K., A.H., M.L. and M.K. collected the data; D.K., J.K. and M.K. analysed the data; D.K., J.K. and M.K. led the writing.

Editor: Ole Vetaas

Appendix S1 Number of sampled plots per location. The total number of plots is indicated after the name of the location.



Chapter 2

Island biogeography disentangles species pool effects from environmental drivers of local β diversity

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Island biogeography disentangles species pool effects from environmental drivers of local β diversity

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ABSTRACT

Using an island size gradient with variation in species pool sizes from small to large pools, we are answering the question: In what way do the species pool and environmental heterogeneity influence local community composition (β diversity) and how are these two aspects linked? Using a hypothesis-driven approach we disentangle the species pool from environmental heterogeneity by separately studying local β diversity of ferns within islands as well as along an island size gradient with increasing species pool sizes. Along the island size gradient, β diversity is driven by the species pool, within islands it is driven by environmental heterogeneity. Explanatory power of environmental heterogeneity depends strongly on the species pool. Using niche overlap between species as well as species abundance based approaches we show that increasing competition at sites with large species pools provides a biotic explanation for how the species pool influences local β diversity.

INTRODUCTION

Explanations of the processes underlying changes in community composition (β diversity) have traditionally focused on the relative importance of local scale ecological mechanisms of community assembly versus regional scale factors determining the sizes of the regional species pools. It has been suggested that β diversity is determined by environmental heterogeneity, the variation in ecological conditions and their interaction with species attributes such as range size (Rodríguez & Arita 2004), dispersal ability (Soininen et al. 2007), as well as in the strength of processes such as habitat filtering (Qian & Ricklefs 2007). In contrast, other studies have proposed that patterns of β diversity are driven by differences in the species pool and hence by factors that vary at larger scales and tickle down to local scales, e.g., habitat area and its attributes as well as evolutionary history, of both the lineages and the regions (Whittaker et al. 2001, Kraft et al. 2011, Lessard et al. 2012) or neutral processes (Hubble 2001). Additionally, it has been hypothesized that within-site biotic interactions might control local species richness and community composition (Tilman 1997 Ecology, Zobel 1997).

Although various studies have found empirical evidence for all of these processes, one major question remains to be answered: In what way do the species pool and environmental heterogeneity influence local β diversity and how are these two aspects linked to each other? To answer this question, disentangling effects of the species pool from ecological mechanisms has proven to be extremely difficult. Most studies exploring β diversity have thus focused on either one of the two aspects, and explanations about their combined impacts remain elusive. This is mainly due to the problem of quantifying change in the species pool, especially if there are no clear boundaries to the geographical extent of the study regions. Most studies on local β diversity thus either share a common species pool or have species pools of local sites that overlap to unknown degrees (e.g. the Amazonian lowlands, Toumisto 2003). While some authors have been using γ diversity as representative for the species pool (eg. Kraft et al 2011), this might not be appropriate in all cases. γ diversity and β diversity are representations of the same phenomenon, namely species richness within a certain area and are not independent of each other. The species pool differs from this somewhat by including species which can potentially occur in local assemblages, but do not necessarily occur and are therefore not included in any richness measure. While at large specie scales γ diversity will be closely correlated with the species pool, at smaller spatial scales it will not necessarily be so. A sharply divined (defined?) inclusion of the species pool in analyzing β diversity remains therefore elusive.

We developed two alternative hypotheses if the regional species pool may influence local β diversity and how this process can be explained. Most basically, the regional species pool determines which species are available to migrate into local assemblages as determined by the availability of appropriate environmental niches (hereafter: niches). At sites with a limited species pool, we would expect to find similar species when comparing two local communities, simply because it is always the same species that migrate into the local communities and fill all possible niches. In contrast, at sites with large species pools, we have two different possibilities. When the pools consist of several species with different niche optima, one would expect to find 'different' species in the different niches. Alternatively, at sites with large species pools consisting several more 'neutral' species sharing niche preferences, based on random sampling from the species pool, one would expect to find different species in similar niches.

These hypothetical situations would lead both to different levels of β diversity and to different relationships of community composition with environmental factors. While in both cases ('neutral' or 'different') β diversity increases with the size of the regional species pool (H1), in the case of small species pool, β diversity would be low even in cases of high environmental heterogeneity. Consequently environmental heterogeneity would not be reflected in species community composition. In the case of a large species pool including species with 'different' niche optima, we would find high β diversity and close relationships of community composition with the environment (H2a). Finally, in large species pools consisting 'neutral' species sharing niche optima, β diversity would still be high but no relation to local environmental conditions would be detectable (H2b).These hypotheses include two different aspects of the regional species pool, namely its size (i.e., the number of species included) and the degree of niche differentiation between the species. These two aspects interact in complex ways to influence both β diversity and its relationship to the environment. In both cases, absence of an increase of β diversity would be possible in cases with such large species pools that local communities are completely different from each other, i.e., in cases where β diversity would be saturated. Accordingly, unsaturated levels of β diversity are a prerequisite to test these hypotheses (e.g. H1 needs to be proven right).

According to these theoretical assumptions we formulated three main hypotheses:

H1: With increasing regional species pool, β diversity increases in accordance to the larger species pool.

H2a: At sites having large species pools and high degrees of niche differentiation β diversity can be explained by environmental heterogeneity.

H2b: At sites having large species pools and low to no degree of niche differentiation β diversity cannot be explained by environmental heterogeneity

To test these hypotheses, we used an island biogeographical approach, based on the well known species-area relationship (Arrhenius 1921). Islands provide optimal study systems to solve the problem of unknown species pool sizes when analyzing patterns of local β diversity, since they comprise well defined study units with specific species pools that vary in accordance to the size of the island (i.e., the species area relationship, Arrhenius 1921, Whittaker 2012 JBI). In the present study, we therefore used island systems to disentangle the effects of varying species pool sizes from those of environmental heterogeneity to answer the question in which way the species pool and environmental heterogeneity influence local β diversity and how they are linked to each other. To do this, we sampled 15 mountain ranges on 12 islands of differing size (116–786,000 km^2) in the Malesian archipelago and New Guinea to span a gradient of habitat area and varying regional species pool size (Fig. 1 A, Table S1). At each site, we sampled fern communities as well as environmental factors in 16 plots of 400 m^2 each, arranged in a spatially fixed design (Fig. 1 B). Using this design, we quantified β diversity as proportional turnover within a habitat per sampling site using multiplicative β-partioning ($1-\alpha/\gamma$) (Whittaker 1960, Tuomisto 2010, Anderson et al. 2011, Kraft et al. 2011). We used three analytical approaches to assess the influence of the explanatory factors on β diversity along the island size gradient: ordinary least square (OLS) regression, multi linear regression and variable importance (Burnham& Anderson 2002), and variance partioning (Tuomisto et al. 2003, Cottenie 2005, Legendre et al. 2009). Within the island

β diversity was assessed using mantel tests, partial mantel tests, and multiple regression on distance matrices (Legendere et al. 2009).

MATERIALS AND METHODS

Study sites. We selected 12 islands of different sizes in Indonesia and the Philippines (Fig. 1). On each island, sampling sites were located at 1100 m and 1200 m within the main mountain range of the island (see Appendix S1). We chose the altitude of 1100-1200 m because, on the one hand, this belt has a high number of fern and lycophyte (henceforth called fern) species (Bhattarai 2004, Carpenter 2005, Kluge & Kessler 2006, Kessler et al. 2011), enabling us to collect statistically relevant samples. On the other hand, human footprint at this elevation is the lowest worldwide (Nogués-Bravo et al. 2008), providing us with mostly undisturbed natural ecosystems. On the large islands New Guinea, Mindanao, and Sulawesi an additional site was selected in a peripheral mountain range, resulting in a total of 15 sampling sites (Table S1).

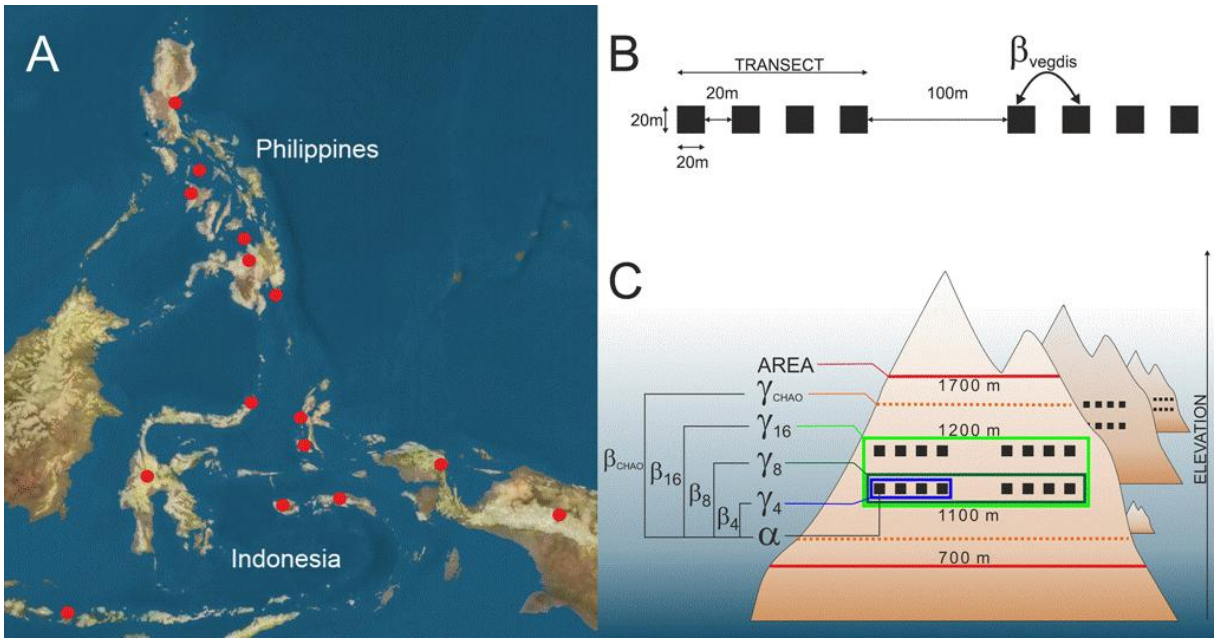

Fig. 1 Sampling design. Sampling locations (red dots) spanning the island size gradient in the Malesian Archipelago and New Guinea (**A**). Schematic representation of the sampling design consisting of 16 plots of 20 x 20 m² each with one transect consisting of four plots at fixed distances of 20 m. Two transects of four plots each were arranged 100 m apart, each at both 1100 m and 1200 m elevation. β_2 was calculated by the mean turnover in species composition between adjacent plots (**B**). Quantification of the mean richness per plot (α diversity), the species pools at different spatial scales (γ diversities), and the respective β diversities as ratios between γ and α diversity. γ_{CHAO} was calculated using a species richness estimator (Chao 2). Habitat area (AREA) was measured as the land surface of each studied mountain range per island between 700 m and 1700 m (**C**).

Ferns as focal plant group.

Ferns are distributed worldwide, and are independent of biotic pollination and distribution vectors because of their spore dispersal (Barrington 1993). The high species richness of ferns allows statistical inference of the documented data, and the relatively lower dependence from biotic vectors link patterns of distribution directly to abiotic factors. As a result, ferns are highly suitable for studying ecological niche structuring (Barrington 1993).

Transect design.

Ferns were sampled in standardized plots of 20 m x 20 m (Fig. 1 B). This plot size has previously been used for surveys of local fern diversity (Kessler 2000, Kluge & Kessler 2005) and is large enough to be representative, but also small enough to be ecologically homogeneous and to allow rapid and efficient surveys (Kessler & Bach 1999). Since β diversity changes with geometric distance (Whittaker 1960, Anderson 2011) we used a fixed sampling design of four plots with a distance of 20 m between adjacent plots. On the different islands, two such transects separated by 100 m were established at 1100 m and two at 1200 m (Fig. 1 C).

Plant sampling.

In each plot, we counted the number of fern species and the abundance of each species. Epiphytic species were surveyed by a combination of climbing on trees, cutting selected branches, looking for fallen branches on the ground, and through the use of binoculars. This approach has previously been successfully applied in studies of this kind (Kessler 2000, Kluge & Kessler 2005, Kessler et al. 2011). Every fern specie in each study region (but not in each plot) was collected for later determination and deposited in the Herbarium Zurich (ZH), Herbarium of the Central Mindanao University (Central Mindanao University Herbarium), Herbarium Bogor (BO), and the Herbarium University of California, Berkley (UC).

Selection of explanatory variables.

Across the island size gradient.

As representative for the species pool, we define area as the total habitat area within a mountain range where the sampling sites were located. For ferns, which have maximum diversity at mid elevations and few lowland species (Bhattarai et al. 2004), the lowlands are dispersal barriers for most species, rendering the mountain ranges the actual habitat islands harboring the species pool. Using the whole surface area of an island would therefore be misleading. Also, for peripheral sampling sites on large islands, usually comprising just a remote mountain range, the whole area of the island would not be representative. Therefore, we calculated habitat area based on the total surface area of the elevational belt ranging from 700 m to 1700 m. This is the elevational range amplitude of the majority of fern species at this elevation (Bhattarai 2004, Carpenter 2005, Kluge & Kessler 2006, Kessler et al. 2011) and allows an approximation of the area from which hosts the species pool local communities are recruited from. We used ArcGis 10 (ESRI 2011) and ASTER GDEM (NASA 2001) to calculate the surface area of the respective elevational bands within the mountain ranges.

Additionally we selected a set of 33 environmental explanatory variables (see Appendix S2) to test a possible environmental influence on the observed patterns of diversity across spatial scales.

We used global temperature and precipitation models of nineteen different climatic variables derived from WorldClim – Bioclim (Hijmans 2005) at a resolution of 30 arc-seconds.

Because the factors potentially covary and the use of 33 explanatory variables (32 environmental plus area) on the observed variable will lead to massive over-parameterization, we reduced the environmental variables for regional climatic conditions (temperature and precipitation), local environmental conditions using Principle Component Analysis (PCA). PCA axes were selected

using a threshold of 70% variance explained (see Appendix S3). Where applicable, variables were standardized for zero mean variance to account for different measuring units.

Within island

To describe turnover within islands, we used a set of 18 environmental factors (see Appendix S2) which vary within the scale of the study site (i.e., one plot or one transect). These factors are not necessarily representative on a larger scale and differ more strongly within sites on one island than large scale factors like precipitation or air temperature. Relative air humidity is a crucial environmental factor for ferns, but measuring it directly over long periods of time is not possible without considerable effort. Therefore, we used bryophyte cover on trees (BRYO) as proxy for relative air humidity following the methodology of Karger et al. (2012) which has been verified for five sites within the Philippines using data loggers for relative humidity for a period of one year. We also included local environmental factors such as mean inclination of the plot (INC) and canopy cover (CAN) that were visually estimated in each plot. Soil samples were taken from every plot and analyzed for 12 different soil parameters (see Appendix S2). Since variation in these factors could be crucial for β diversity, we also calculated the variation between plots of each variable for all study sites.

Diversity at different spatial scales.

Divining β diversity requires measuring species diversity at different spatial scales (eg. α and γ diversities). We therefore measured α diversity as the mean richness per plot of 20 m x 20 m ($\alpha = \bar{S}$) to avoid spatial pseudoreplication. γ_4 diversity was then defined as the total number of species found in all 4 plots per transect, γ_8 diversity as the total number of species found in two transects of a total of 8 plots, and γ_{16} diversity as the total number of species found in four transects of a total of 16 plots. γ_{CHAO} diversity was calculated using the Chao 2 estimator (Chao 1984) using γ_{16} diversity. γ_{reg} diversity was defined as the total number of fern species on an island or in a given elevational belt and quantified as the total number of species listed in the Flora Malesiana (Kalkman & Noteboom 1998).

β diversity was defined as proportional turnover within a habitat per sampling site for the respective spatial scale of γ (x = 4, 8, 16, CHAO) ($1 - \alpha / \gamma_x$) (Kraft et al. 2011, Anderson et al. 2011, Whittaker 1960, Tuomisto 2010). This captures turnover on a very small scale within a habitat. β diversity can, however, be calculated in numerous ways (Koleff et al. 2003, Tuomisto 2010 a, b). Therefore, we also calculated all indices listed by Koleff et al. (2003). The different indices were strongly correlated and resulted in quantitatively similar results (median $R^2 = 0.99$, $p < 0.001$ in comparing indices). For the sake of clarity, we therefore only present here the results of proportional turnover.

Spatial scale

The term "scale" in this context refers to the size of the units used in the sampling of assemblages (Whittaker et al. 2001) and in our case ranges from 400 m² (alpha) to the whole mountain ranges (Fig. 1). The largest scale (γ_{reg}) differs in spatial scale from the smaller more local scales ($\alpha - \gamma_{CHAO}$), by being a more regional scale based on the size of the respective island, and therefore has not been included in the analysis of local β diversity. It has been included to confirm an increase in diversity with an increase in habitat area.

Statistical analyses

Across the island size gradient

We used ordinary least square regression to identify single predictors of the different diversity levels for within island turnover and turnover along the island size gradient. However, the different diversity levels are more likely to be influenced by several factors, so that, e.g., the upper limits of α diversity along an elevational gradient might be restricted by low temperatures while the lower limits are restricted by low humidity (Bhattarai et al. 2004, Kluge et al. 2006, Kessler et al. 2001). Since in most cases we expected these combined effects of different independent variables, we used multiple linear regression with all possible variable combinations of the reduced PCA-axes to build full linear models. Since using all variables within a model might lead to over-parameterisation, we used stepwise variable reduction on the full linear models based on AIC values to build reduced linear models. Additionally, we performed a subsequent analysis using variation partioning (Toumisto et al. 2003, Cottenie 2005, Legendre et al. 2009) including the three variables with the highest significance as explanatory variables and the variable of the respective diversity level as response variable.

To test if environmental heterogeneity changes systematically across islands, we calculated the area which islands occupy within an n-dimensional hypervolume spanned by all environmental variables using Principal Component Analysis (PCA).

Within island

To test if environment and spatial distance affect within island turnover, we used a combined approach of partial mantel tests and multiple regression on distance matrixes (Tuomisto 2003, Legendre 2009). Distance matrixes for turnover were calculated using the same measurement as along the island size gradient (proportional turnover = $1-\alpha/\gamma$). To build explanatory matrixes we combined ecological factors to a distance matrix containing all 12 soil parameters as well as bryophyte cover, inclination, and canopy cover (ECO). Parameters were standardized to zero mean variance to account for different measuring units. A spatial distance matrix (DIST) was built using the geographical distance of the plots.

In addition, we checked for sampling intensity to rule out a possible influence of undersampling on the observed patterns (Toumisto & Ruokolainen 2012) by calculating species accumulation curves for each site using three different approaches, by adding up species per site as they were collected, by randomly adding up species per sites, and by adding up individuals instead of sites.

All analyses were conducted using R 2.13.1 (R Development Core Team 2011).

Indicators for dominance and competition

To test H2a and H2b we calculated the mean niche overlap of all species present at one site using the Pianka index (Pianka 1975). Instead of defining the niche using measured environmental parameters, this methodology assumes that species occurring within a plot share a common niche in respect to all environmental parameters within the plot. A smaller niche overlap between species can be used as indicator for competitive exclusion (Pianka 1975) and indicates niche differentiation between species. The theoretical assumptions formulated in the hypotheses also predict a shift in relative species abundance of a species. To test this we calculated the mean number of individuals per species.

While only indirect indicators for competition can be derived from our data, dominance can easily be quantified by giving weight to species abundances (Toumisto 2012 Oikos). Calculating the dominance of species will show if competition is equal between species or if a few species are able to outcompete many. This allows to test if the observed patterns are only due to the abundance of a few dominant species. All measurements for dominance and competition were based on calculations performed on the basis of 16 plots.

RESULTS

Across the island size gradient

With the exception of α diversity, all levels of diversity showed an increase with AREA (Fig. 2). α diversity showed no relation to area. The OLS showed several single predictors for the different levels of diversity among which AREA was the most important (See Appendix S4). Local inclination (INC) also showed high correlations with most diversity levels; it,is, however, the only factor that is strongly autocorrelated with AREA. Several soil parameters showed high correlations with α and γ diversities, but were negligible for β diversities (see Appendix S4).

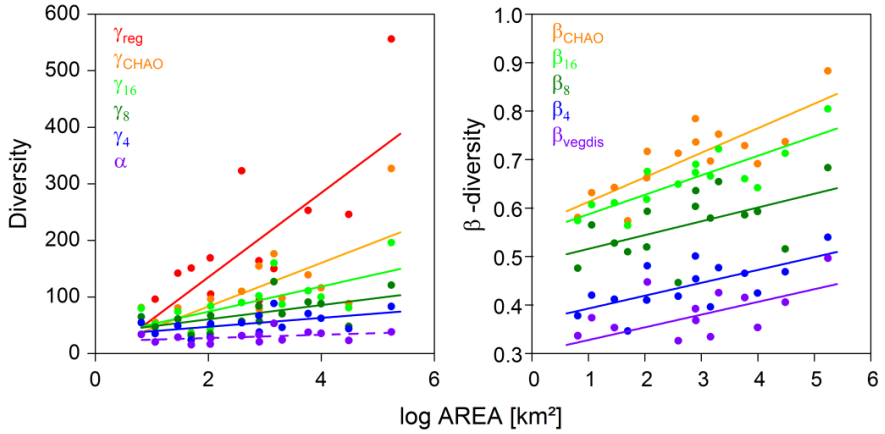

Fig. 2 Diversity patterns across spatial scales along the island size gradient. Trendlines were fitted using ordinary least square regression (OLS). Significant relationships are shown with uninterrupted lines, while non significant relationships are indicated with interrupted lines.

The multiple linear regression with stepwise variable reduction (MLR) showed similar results to the OLS. AREA appeared as significant exploratory variable in all models for the different scales of β diversity (See Appendix S5). For α and γ diversities, ecological variables were more significant than AREA, which only appeared to be significant for γ16 and γ_{CHAO}. Predictive power of the models ranged from moderate (R^2_{adj} = 0.24, p = 0.035, β8) to strong (R^2_{adj} = 0.74, p = 0.001, γ_{CHAO}).

The same pattern appeared when we calculated variable importance. AREA was important at all scales of β diversity but only of minor importance for α and γ diversity (FIG. 3, also see Appendix S6). Ecological variables were, however, of main importance for α and γ diversity. The importance of AREA for β diversity seemed to increase with increasing spatial scale, while the importance for ecological variables (ECO3) on α and γ diversity decreased with spatial scale.

This contrasting pattern also appeared in the results of the variance partioning (Fig. 3, see Appendix S7). AREA explained up to 45 % of the variation in β diversity (β16) and ecological factors (ECO3) explained up to 48 % in α and γ diversity (α). AREA explained hardly any variation as single factor for α and γ diversity but in combination with ecological factors explained up to 35 % of the variation. The amount of unexplained variance, however, was in

general higher for β diversities as for α and γ diversities. Unexplained variance also decreased with increasing spatial scale for β diversity whereas it remained almost the same across all scales for α and γ diversity.

Environmental heterogeneity did not change systematically with AREA across the island size gradient (OLS, $R^2 = 0.03$, $p=0.487$).

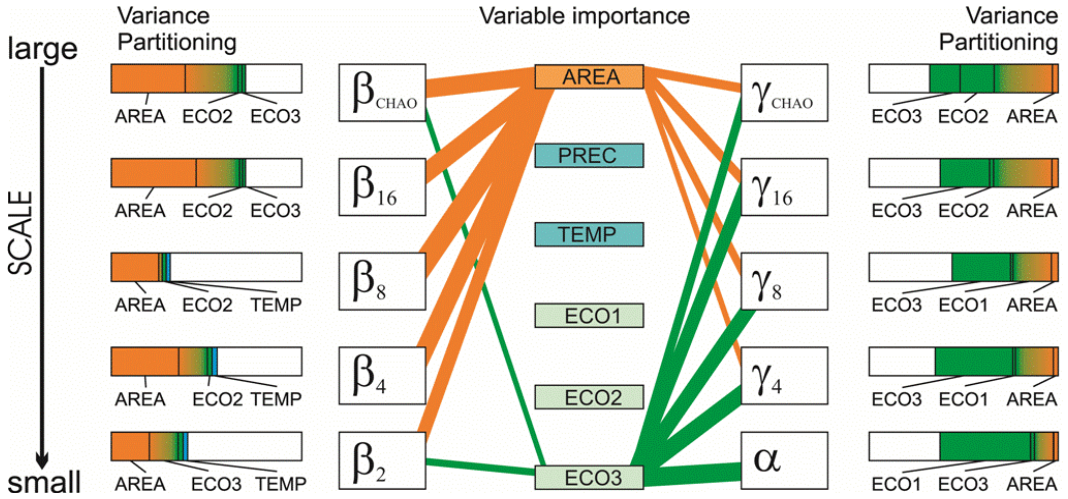

Fig. 3 Factors related to the different levels of diversity and percentage of variance explained by the three most important factors along the island size gradient. Results of multimodel inference are shown in the center, with the thickness of the lines corresponding to the relative variable importance. Results of variance partioning are shown at the left (β diversities) and right (α and γ diversities) edges, with the size of the corresponding area equivalent to the percentage of variance explained by the respective factors. Large scale factors are highlighted in orange (habitat area) and blue (ecological), and small scale factors in green; the white area relates to the percentage of unexplained variance. AREA = surface area of mountain range (habitat area) PREC = precipitation, TEMP = temperature, ECO1 – ECO3 = ecological variables PCA axis, Graduations between green and orange indicate the variance explained by two factors.

Within the islands

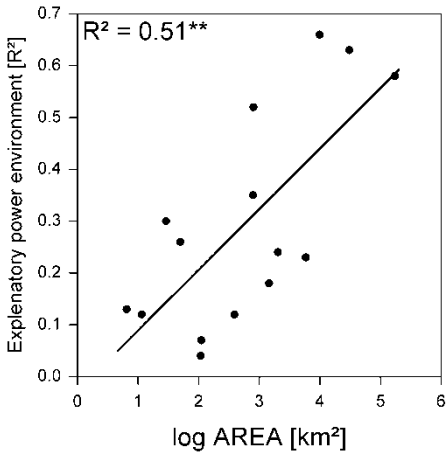

Fig. 4 Explanatory power (R^2) of the multiple regression on distance matrices (MRM, black dots) plotted over area.

Environmental variables significantly explained β diversity within each of the sampling sites, the only exception being Mt. Hamiguitan on Mindanao Island (see Appendix S8). Explanatory power of the MRM ranged from 0.07 (Bacan) to 0.66 (New Guinea – Arfak). Similar results were obtained using Mantel tests and partial Mantel tests, but only on six islands were significant results obtained. Taking geographical distance into account in the partial Mantel tests did not significantly change the explanatory power of environmental variables on β diversity. Explanatory power of the MRM and the Mantel test significantly increased with AREA (Fig. 4) showing highest explanatory power on large islands than on small islands. Species accumulation curves showed that diversity levelled off after approximately sampling four to eight plots, showing that a significant amount of the local flora was sampled (see Appendix S9). All three different methods to calculate species accumulation curves resulted in similar results.

Indicators for dominance and competition

Niche overlap as main indicator for competition among species significantly decreased with AREA (R^2 = 0.65, p=0.001) showing an increase in competition between species on larger islands (Fig. 5). In line with this, the mean abundance per species decreased with AREA (R^2 = 0.60, p=0.001). The effective number of species, which takes the abundance of species into account showed an increase in species with AREA (R^2 = 0.34, p= 0.02).

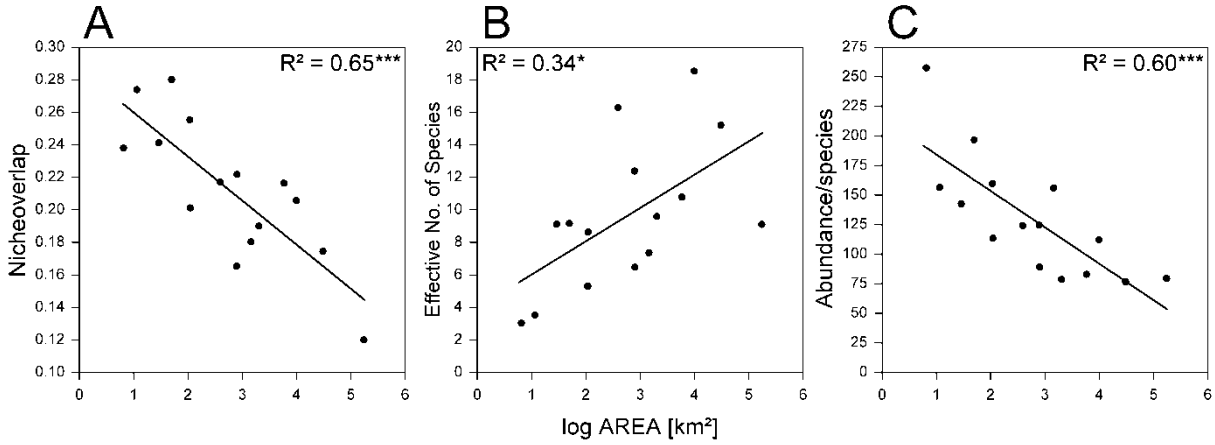

Fig. 5 Indicators for competition and dominance along the island size gradient. **A** Mean niche overlap between species. **B** Effective number of species when equal abundance is given to all species. **C** Mean abundance per species. Trendlines were fitted using linear least square regression. Significance codes: *≤0.05,***≤0.001.

DISCUSSION

Using islands as study systems, we were able to successfully disentangle the effect of the species pool size from those of environmental heterogeneity and answer in what way they interact to influence local β diversity. All analytical approaches showed that β diversity along the island size gradient was mainly related to area and that the influence of ecological factors was very limited overall (Fig. 3). This confirms the initial hypothesis (H1) that the species pool has influence and alters patterns in local β diversity. The increase in within island local β diversity can therefore be directly linked to an increasing species pool (Fig. 6). Using different approaches (OLS, multiple regression, and variance partioning) shows that the observed patterns are fairly robust, and not dependent on any analytical difference between approaches or possible interactions between environmental factors (Fig. 3).

In contrast however, β diversity within the islands was strongly determined by environmental heterogeneity within an island (Fig. 4). This confirms that β diversity is significantly influenced by both these two major components; first the size of the regional species pool which changes with habitat area as described by the species-area relationship (Fig. 2), and second environmental heterogeneity (Fig. 4). Both of these influences have previously been shown in numerous studies, but usually only separately for species pool effects (Kraft et al 2011) or environmental effects (Tuomisto 2001), and have not been disentangled to draw a combined conclusion of their effects on community composition.

Distinguishing between H2a and H2b allows interpretation in which way the species pool influences local β diversity of local communities within the islands. The sites with large species pools show a higher degree in explanatory power of the environment than the sites with small

species pools. This increase can be linked to an increasing niche differentiation in large species pools and confirms H2a. At the same time we can reject the more 'neutral' hypothesis H2b which would have resulted in no explanatory power of environmental heterogeneity on β diversity along the island size gradient. Other indicators which favor H2a over H2b are the decrease in niche overlap and the decrease in mean abundance per species with increasing species pool size (Fig. 5). We interpret this in a way that species are pushed into their preferred environmental niches and are outcompeted in lesser preferred niches when competition increases with an increase in the species pool. This increase in competition seems to be rather constant and is not driven by a few species outcompeting many (Fig. 5), a conclusion which can be directly drawn from the increase in the effective number of species which takes species abundances into account (Tuomisto 2012). Altogether this allows us to draw a tentative conclusion how local communities are assembled (Fig. 6).

The size of the habitat area determines the size of the regional species pool from which species migrate into local communities. The environmental conditions within local communities determine which species from the species pool into local communities find appropriate niches (Fig. 6). Competition pushes species into their preferred niches and seems to be the primary force which gives a biotic explanation in which way a larger species pool influences local β diversity. How many species are found within a community (alpha and gamma diversity) is, however, set by local environmental conditions as well as the surrounding species pool (FIG Fig. 3). While local environmental conditions determine how many individuals can grow within a local community and therefore set an upper limit on the number of species (species saturation Srivastava 2001), the regional species pool influences local richness by the mass effect (Grytnes and Vetaas, Karger et al 2011). An increase in diversity with increasing species pool size could only be measured for γ scales, but not for α scale (Fig. 2). Therefore the mass effect on α and γ diversity seems to depend on spatial scale.

The effect of the species pool on local β diversity on the other hand does not seem to be scale dependent, as β diversity increases in similar rates across spatial scale with increasing species pool sizes (Fig. 2). This is somewhat surprising taking into account that α and γ diversity show scale-dependent responses to changing species pool sizes (Fig. 2). We also found that the relative influence of area on β diversity decreased with decreasing spatial difference between α and γ diversity (Fig. 3) leading to a high amount of unexplained variance of β diversity. While we cannot completely exclude the possibility that part of the unexplained variance may be due to unmeasured ecological factors, we consider this to be unlikely since the amount of unexplained variance did not show any change with spatial scale for α and γ diversity. Therefore the observed increase of unexplained variance might be due to a higher random distribution of species at smaller spatial scales where environmental conditions are more homogeneous between plots.

In contrast to the patterns observed along the island size gradient, within sites (islands) β diversity is strongly determined by environmental heterogeneity within the sampling sites (Fig. 4) as indicated by previous studies (Tuomisto et al. 2003, Jones et al. 2006, Jones et al. 2011, Higgins et al. 2011). This dependence of β diversity on the environmental heterogeneity seems to be, however, dependent on the surrounding habitat area which harbors the regional species pool. Only sites with large species pools showed strong dependents of β diversity on environmental heterogeneity whereas at sites with small species pools environmental heterogeneity explained only small amounts of the observed β diversity. The amount of local environmental heterogeneity, however, did not change systematically with habitat area nor was it in general higher on large islands than on small islands. While larger islands certainly tend to have larger

variation in environmental conditions, this is only true at a regional scale and is not relevant at the scale of our 16 study plots, which spread over an area of about 1 km^2. At a local scale where the amount of sample area is the same, there is no theoretical basis why larger islands should show higher variability in environmental conditions than small islands. With respect to unexplained variance, our analysis shows therefore, that high degrees of unexplained variance in analyzing β diversity (or random patterns) can either be resulting from small sampling scales or small overall species pools and reduced competition.

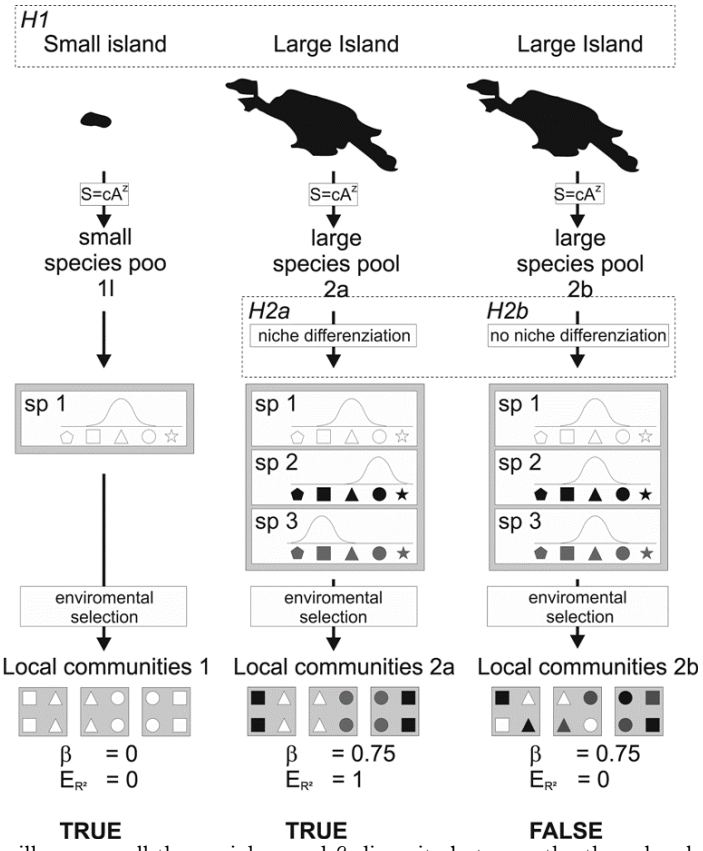

FIG. 6 Simplified example how different species pool sizes influence β diversity in local communities. The specific hypotheses tested are indicated in italic and dashed lines. We show three different regional species pools: pool 1 (left) consists of only one species (sp 1, white) that can occur in five different environmental niches (niche symbols = square, triangle, circle, polygon, star). sp 1 has its niche optimum and maximum competitive strength in the middle niche (triangle) as represented by the curve above the niche symbols, and is less competitive in the other niches (circle, square). Regional species pool 2a (middle) consists of three species with 'different' niche optima. The additional species (sp 2 and sp 3) are more strongly competitive in the square niche (sp 2) or respectively in the circular niche (sp 3). Regional species pool 2b (right) shows an alternative version of 2a consisting of three 'neutral' species with similar niche optima. These regional species pools form the basis from which local communities are composed at three habitats in each island. These local habitats have similar environmental heterogeneity in all islands, as shown by the similar niche symbols. In the case of regional species pool 1, the only available species (S1) will occupy all three niches and β diversity between the three local communities will be zero. In the case of regional species pool 2a, each of the three species will find its preferred environmental niche and outcompetes the other species in its preferred niche. This results in communities that are formed by different species so that β diversity is higher than in the case of a small species pool. At the same time, α diversity (α) stays the same in all local communities while the mean abundance of each species (Abu) declines. If β diversity is now analyzed for the explanatory power of environmental heterogeneity (E_R^2), in local communities 1a (left) it will have no explanatory power, while it explains all β diversity in local communities 2a (middle). In the case of a 'neutral' local community with shared niche preferences, environmental heterogeneity has no explanatory power even with an increase in the species pool (right).

In conclusion, we are finally able to answer the question: In what way do the species pool and environmental heterogeneity influence local β diversity and how are these two aspects linked to each other? We show that changes in local β diversity are driven in combination with the species pool as well as ecological heterogeneity. To which degree environmental heterogeneity explains β diversity depends, however, on the size of the species pool with only sites with large species pools showing high explanatory power of environmental heterogeneity. In contrast, at sites with small species pools, the distribution of species is more random than expected from environmental heterogeneity. Explanations for these patterns can be found in the increasing competition for available niches between species at sites with large species pools. This has major implications for studying local community composition, showing that β diversity is determined by

two major processes, the size of the species pool, and environmental heterogeneity. Aside from providing a neat explanation of local community assembly, the shown processes are of special importance for the determination to what degree either random distribution (stochastic processes) or environmental heterogeneity (deterministic process) explains β diversity. Also increasing competition with increasing species pool sizes gives a biotic explanation with respect to niche preferences, on how local community assembly is influenced by processes at larger spatial scales which determine the size of the regional species pool.

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SUPPORTING INFORMATION

Appendix S1 Locations of the sampling sites and elevations in Indonesia and the Philippines.

Island	Mountain/Site	Latitude	Longitude	Elevations sampled
Luzon	Mingan Mountains	15°25'N	121°24'E	1100 m, 1200 m
Sibuyan	Mt. Guiting Guiting	12°26'N	122°33'E	1100 m, 1200 m
Panay	Mt. Madia-as	11°21N	122°08'E	1100 m, 1200 m
Camiguin	Mt. Timpoong	09°11'N	124°42'E	1100 m, 1200 m
Mindanao	Mt. Kitanglad	08°08'N	124°55'E	1100 m, 1200 m,
Mindanao	Mt. Hamiguitan	06°44'N	126°10'E	1100 m, 1200 m
Sulawesi	Toro , Lore Lindu NP	01°29'S	120°03'E	1100 m, 1200 m
Sulawesi	Gunung Duasudara	01°29'N	125°09'E	1100 m, 1200 m
Tidore	Gunung Kiematubu	00°40'N	127°24'E	1100 m, 1200 m
Bacan	Gunung Sibela	00°42'S	127°31'E	1100 m, 1200 m
Buru	Wafehai	03°13'S	126°34'E	1100 m, 1200 m
Seram	Manusela NP	02°59'S	129°11'E	1100 m, 1200 m
Lombok	Gunung Rinjani	08°20'S	116°24'E	1100 m, 1200 m
New Guinea	Pass Valley	03°46'S	139°14'E	1100 m, 1200 m
New Guinea	Arfak Mountains	01°20'S	134° 8'E	1100 m, 1200 m

Appendix S2 Explanatory factors used in the analysis of β diversity along the island size gradient and within islands. Usage of an explanatory factor in the specific analysis is indicated by + (included) or – (not included).

		Used in analysis	
Explanatory factor	**Abbreviation**	**Island size gradient**	**Within island**
log Habitat area [km²]	AREA	β,α,γ	-
Precipitation [PCA]	PREC	β,α,γ	-
Temperature [PCA]	TEMP	β,α,γ	-
Bryophyte cover on trees [%]	BRYO	β,α,γ	β
Variation in Bryophyte cover on trees [%]	$BRYO_{var}$	β,α,γ	β
Mean Inclination [°]	INC	β,α,γ	β
Variation in mean Inclination [°]	INC_{var}	β,α,γ	β
Canopy cover [%]	CAN	β,α,γ	β
Variation in Canopy cover [%]	CAN_{var}	β,α,γ	β
Soil carbon content [mmol/g]	Ctot	β,α,γ	β
Soil nitrogen content [mmol/g]	Ntot	β,α,γ	β
Carbon/nitrogen ratio	CN	β,α,γ	β
Base saturation [%]	Base	β,α,γ	β
Nitrogen ion content [µmolc/g]	Na	β,α,γ	β
Aluminium ion content [µmolc/g]	Al^{3+}	β,α,γ	β
Calcium ion content [µmolc/g]	Ca^{2+}	β,α,γ	β
Iron ion content [µmolc/g]	Fe^{2+}	β,α,γ	β
Kalium ion content [µmolc/g]	K^{+}	β,α,γ	β
Magnesium ion content [µmolc/g]	Mg^{2+}	β,α,γ	β
Manganese ion contetn [µmolc/g]	Mn^{2+}	β,α,γ	β
Natrium ion content [µmolc/g]	Na^{+}	β,α,γ	β
Spatial distance between plots [m]	DIST	-	β
Variation in soil carbon content [mmol/g]	$Ctot._{var}$	β	-
Variation in soil nitrogen content [mmol/g]	$Ntot._{var}$	β	-
Variation in Carbon/nitrogen ratio	CN_{var}	β	-
Variation in Base saturation [%]	$Base_{var}$	β	-
Variation in Nitrogen ion content [µmolc/g]	Na_{var}	β	-
Variation in Aluminium ion content [µmolc/g]	$Al^{3+}{}_{var}$	β	-
Variation in Calcium ion content [µmolc/g]	$Ca^{2}{}_{var}$	β	-
Variation in Iron ion content [µmolc/g]	$Fe^{2}{}_{var}$	β	-
Variation in Kalium ion content [µmolc/g]	K_{var}	β	-
Variation in Magnesium ion content [µmolc/g]	$Mg^{2}{}_{var}$	β	-
Variation in Manganese ion content [µmolc/g]	$Mn^{2}{}_{var}$	β	-
Variation in Natrium ion content [µmolc/g]	Na_{var}	β	-

Appendix S3 Eigenvalues and cumulative proportion explained (cum. prop. expl. [%]) for variable reduction using principal component analysis (PCA). Only axis used in the analysis are shown.

Variable Set		**PC1**	**PC2**	**PC3**	**PC4**
Temperature	eigenvalue	338800	-	-	-
(TEMP)	cum. prop. expl.	0.73	-	-	-
Precipitation	eigenvalue	32730	-	-	-
(PREC)	cum. prop. expl.	0.90	-	-	-
local Ecology	eigenvalue	5.264	4.0373	1.9853	-
(ECO)	cum. prop. expl.	0.35	0.62	0.75	-
local Ecology Variation	eigenvalue	3.644	2.6575	2.1947	1.9827
(ECOVAR)	cum. prop. expl.	0.24	0.42	0.57	0.70

Appendix S4 R^2 values of the OLS. PREC = Precipitation PCA, TEMP = Temperature PCA, AREA = surface Area of the mountain range, BRYO = Bryophyte cover on trees a proxy for relative humidity, INC = Inclination, CAN = canopy closure, C = soil carbon content, N = soil nitrogen content, CN = Carbon/Nitrogen, Base = soil base content, Na = soil natrium content, Al_{3+} = soil aluminium ion content, Ca_{2+} = soil calcium ion content, Fe_{2+} = soil iron ion content, K^+ = soil kalium ion content, Mg2+ = soil magnesium ion content, Mn2+ = soil mangan ion content, Na+ = soil natrium ion content. the subscript 'var' indicates variation, the subscript 'tot' indicates the total amount of the soil component was used. Significance codes: *≤0.05,** ≤0.01,***≤0.001.

	PREC	**TEMP**	**AREA**	**BRYO**	**$BRYO_{var}$**	**INC**	**INC_{var}**	**CAN**	**CAN_{var}**	**C_{tot}**	**N_{tot}**
β_2	0.02	0.05	**0.32***	0.07	0.07	0.14	0	0.04	0.02	0.11	0.09
β_4	0	0.01	**0.45****	0.13	0.09	0.17	0	0.08	0.05	0.13	0.11
β_8	0	0.01	**0.30***	0.15	**0.29***	0.2	0.08	0.06	**0.31***	0.03	0.01
β_{16}	0.03	0.01	**0.70*****	0.09	0.14	**0.31***	0	0.03	0.07	0.15	0.12
β_{CHAO}	0.01	0.02	**0.67*****	0.05	0.08	**0.31***	0	0.05	0.11	0.19	0.15
α	0.06	0.02	0.14	**0.44****	0.06	**0.39***	0.08	0.07	0	0.01	0.01
γ_4	0.06	0.01	**0.29***	0.25	0.02	**0.48****	0.09	0.06	0	0.07	0.05
γ_8	0.03	0.01	**0.33***	0.15	0	**0.53****	0.04	0.06	0.04	0.06	0.04
γ_{16}	0.01	0	**0.46****	0.09	0	**0.56****	0.09	0.02	0.03	0.22	0.16
γ_{CHAO}	0.03	0	**0.49****	0.02	0	**0.47****	0.13	0	0.08	**0.42****	**0.34***
γ_{reg}	0.05	0.01	**0.49****								
	CN	**Base**	**Na**	**Al_{3+}**	**Ca_{2+}**	**Fe_{2+}**	**K^+**	**Mg_{2+}**	**Mn_{2+}**	**Na^+**	**$C_{tot.var}$**
β_2	0.01	0.01	0.03	0.01	0.03	0.06	0.13	0.03	0.09	0	0.03
β_4	0.02	0.01	0.06	0.01	0.04	0.05	0.2	0.02	0.01	0	0.04
β_8	0.04	0.01	0	0.01	0	0	0.04	0.05	0	0.02	0
β_{16}	0.02	0.02	0.04	0.03	0.02	0.16	**0.30***	0.05	0	0	0
β_{CHAO}	0.04	0.03	0.05	0.04	0.02	0.15	0.23	0.06	0	0.02	0.02
α	0.01	0.08	0.02	**0.28***	0.03	0.02	0.01	**0.31***	0.08	0.02	0.01
γ_4	0	0.08	0	0.24	0.02	0.06	0	**0.29***	0.05	0.05	0.03
γ_8	0.01	0.08	0.01	0.21	0.03	0.04	0	**0.29***	0.03	0.02	0.02
γ_{16}	0.04	0.06	0	0.15	0.01	0.16	0.04	0.2	0	0.09	0.01
γ_{CHAO}	0.12	0.03	0.01	0.07	0	0.22	0.09	0.1	0.02	0.21	0.03
	$N_{tot.var}$	**CN_{var}**	**$Base_{var}$**	**Na_{var}**	**Al_{3+var}**	**Ca_{2var}**	**Fe_{2var}**	**K_{var}**	**Mg_{2var}**	**Mn_{2var}**	**Na_{var}**
β_2	**0.28***	0.02	0.07	0.02	0.02	0.04	0.02	0.04	0.16	0.03	0.01
β_4	0.2	0	0.03	0.02	0.02	0.04	0.04	0.05	0.22	0.09	0
β_8	0.01	0.11	0	0.01	0	0.01	0	0.02	0.08	0.1	0.01
β_{16}	0.06	0.03	0.02	0.05	0.03	0.1	0.13	0.1	0.19	0.24	0.02
β_{CHAO}	0.09	0.02	0.01	0.02	0.02	0.05	0.15	0.04	0.24	0.22	0
α	0.02	0	0.2	0.01	**0.52****	0	0.02	0.03	**0.39***	0.02	0.01
γ_4	0.07	0	0.13	0.01	**0.35***	0	0.06	0.01	**0.43****	0.08	0.01
γ_8	0.03	0.03	0.16	0.02	**0.34***	0	0.04	0.03	**0.36***	0.13	0
γ_{16}	0.05	0.02	0.17	0	**0.30***	0.01	0.17	0	**0.30***	**0.30***	0
γ_{CHAO}	0.07	0.02	0.08	0	0.11	0.01	0.26	0	0.2	**0.45****	0

Appendix S5 Results of the multiple linear regressions with stepwise variable reduction along the island size gradient. Best model weighted on AIC values are shown. Significance values (p model) are given for the respective model. Significance codes for model components: '≤0.1, *≤0.05,** ≤0.01,***≤0.001.

Diversity	Model	R^2	Adj. R^2	p (model)
β_2	TEMP+AREA*	0.41	0.32	0.040
β_4	AREA**	0.45	0.41	0.006
β_8	AREA*	0.30	0.24	0.035
β_{16}	PREC+AREA***	0.74	0.69	0.000
β_{chao}	AREA***	0.67	0.64	0.000
α	ECO1'+ECO2***	0.66	0.60	0.002
γ_4	AREA+ECO1+ECO2**	0.71	0.63	0.003
γ_8	AREA+ECO1+ECO3*	0.66	0.56	0.007
γ_{16}	AREA'+ECO2+ECO3**	0.74	0.67	0.001
γ_{chao}	TEMP+AREA*+ECO2*+ECO3*	0.81	0.74	0.001
γ_{reg}	TEMP+AREA**+ECO2***+ECO3*	0.95	0.92	0.000

Appendix S6 Variable importance for all variables used in the multiple regression along the island size gradient.

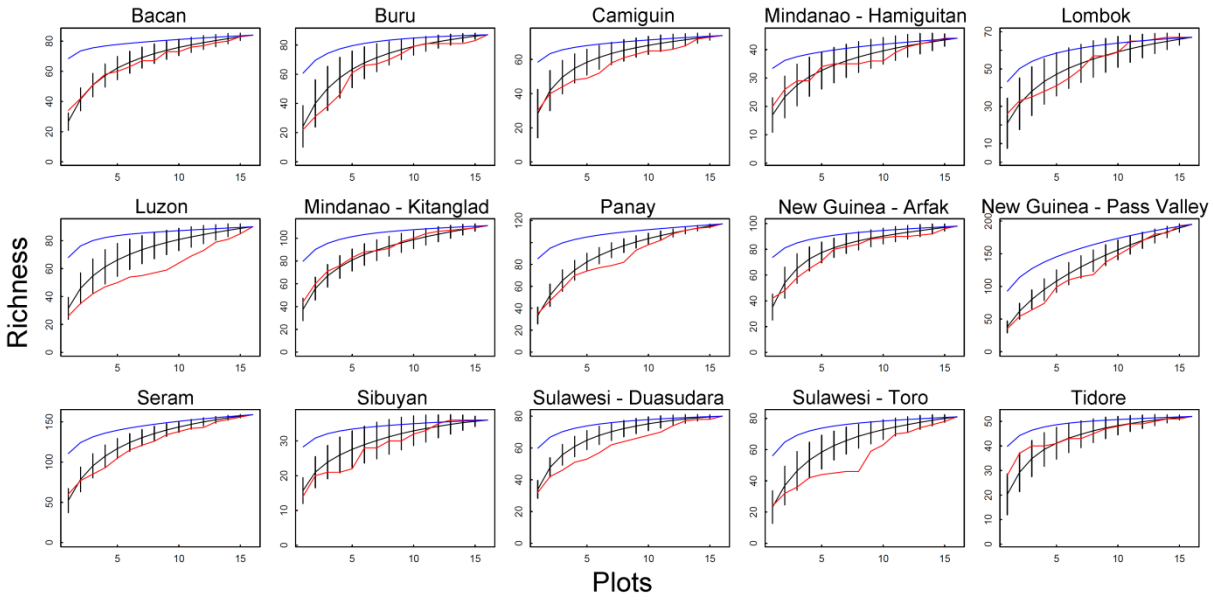
Diversity	ECO1	ECO2	ECO3	PREC	TEMP	AREA
β_2	0.01	0.04	0.27	0.06	0.14	0.49
β_4	0.02	0.04	0.19	0.01	0.06	0.68
β_8	0.01	0.02	0.08	0.01	0.05	0.82
β_{16}	0.01	0.07	0.15	0.07	0.01	0.69
β_{CHAO}	0.01	0.09	0.2	0	0.01	0.70
α	0.13	0	0.71	0.05	0.01	0.10
γ_4	0.08	0.02	0.64	0.04	0.01	0.21
γ_8	0.10	0.02	0.56	0.02	0.01	0.29
γ_{16}	0.03	0.13	0.48	0.01	0.01	0.35
γ_{CHAO}	0	0.28	0.32	0.02	0.02	0.36

Appendix S7 Results of the variance partioning using the three explanatory variables with the highest importance for the different levels of diversity along the island size gradient. Combined variance explained reefers to variance explained by AREA in combination with the two other variables.

Diversity	ECO1	ECO2	ECO3	TEMP	PREC	AREA	combined
β_2			0.02	0.08		0.19	0.15
β_4		-0.02		0.02		0.34	0.15
β_8		-0.07		-0.04		0.24	0.05
β_{16}		-0.03	-0.01			0.45	0.23
β_{CHAO}		-0.02	0.02			0.37	0.28
α	0.07		0.48			-0.03	0.11
γ_4	0.03		0.41			0.03	0.21
γ_8	0.04		0.28			0.06	0.21
γ_{16}		0.05	0.26			0.09	0.33
γ_{CHAO}		0.18	0.17			0.09	0.35

Appendix S8 Results of the Mantel, partial Mantel (controlling for spatial distance (DIST)) and Multiple Regression on Distance Matrices (MRM) for within island β diversity explained by environmental heterogeneity. Islands are arranged by the size of the respective mountain range from small to large. Significance codes: *≤0.05,** ≤0.01,***≤0.001.

	MRM	**Mantel**	**partial Mantel**
Island-(Mountain)	**R^2**	**R**	**R**
Sulawesi - Duasudara	0.13**	-0.13	-0.13
Tidore	0.12**	-0.09	-0.12
Camiguin	0.30***	0.15	-0.05
Sibuyan	0.26*	0.27	0.25
Hamiguitan	0.04	-0.19	-0.21
Bacan	0.07*	0.46***	0.43***
Luzon	0.12*	0.18	0.1
Panay	0.35***	-0.03	-0.04
Lombok	0.52***	0.18	0.09
Seram	0.18**	0.54**	0.51**
Buru	0.24***	0.47***	0.34**
Mindanao	0.23*	0.27	0.22
New Guinea Arfak	0.66***	0.39***	0.36***
Sulawesi- Toro	0.63***	0.29***	0.33***
New Guinea Pass Valley	0.58***	0.35**	0.40**



Appendix S9 Species accumulation curves for all sampled sites. Black lines indicate that species were pooled by random selection of plots, horizontal black lines reffer to the deviation of random estimates. Red lines indicate that species were pooled as they were sampled. Blue lines indicate that species abundances were pooled.

Chapter 3

The theory of island biogeography from regional to local scales: evidence for a spatially scaled echo pattern on fern diversity in the Southeast Asian archipelago

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The theory of island biogeography from regional to local scales: evidence for a spatially scaled echo pattern on fern diversity in the Southeast Asian archipelago

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Keywords Island Biogeography, the equilibrium theory of island biogeography, echo pattern, local diversity, regional diversity, spatial scale, ferns.

Aim To investigate if the equilibrium theory of island biogeography is equally applicable at regional and local spatial scales and if the echo pattern influences local diversity equally across a range of sampling scales.

Location Twelve mountain regions on islands of different sizes, isolation and environmental conditions in Indonesia and the Philippines.

Methods We sampled ferns in standardized field plots in a fixed spatial design at seven different spatial scales (plot to island). We used the two main components of the theory of island biogeography, area and isolation, in combination with local and regional environmental factors to test their predictive power on diversity at the different scales using ordinary least square regression and relative variable importance.

Results The equilibrium model of MacArthur and Wilson applied best at regional scales. The explanatory power of area increased with spatial scale except at the most local scale. The strength of the negative relationships among diversity and isolation decreased with increasing spatial scale. We found evidence for an echo pattern at large to intermediate but not at small spatial scales.

Main conclusions The two main components of the theory of island biogeography, area and isolations, are good predictors of biodiversity at regional scales. The species pool has a scale dependent influence on diversity and is unimportant at the local scale where environmental conditions are better predictors of diversity. To make predictions about diversity on islands it is therefore important to take the scale dependence of the echo pattern into account.

INTRODUCTION

Island systems have long played a crucial role in biogeographical and biodiversity research because they provide comparatively simple systems with clearly defined subunits of usually varying sizes and ecological conditions (Whittaker 1998). The classical equilibrium theory of island biogeography predicts that the number of species that occur on an island is mainly dependent on two factors: the surface area of the island and its isolation (MacArthur and Wilson 1967), although current models may also consider island age (Whittaker et al. 2008).

The principal effect of isolation on species richness results from an inverse relationship with the probability of dispersal to an island, influencing the chance of colonization (MacArthur and Wilson 1967). Particularly on small and less isolated islands, the continuous arrival of propagules might in addition increase population viabilities of species present on the island via a 'rescue effect' (Brown and Kodric-Brown 1977). Consequently, overall species richness should be negatively correlated to island isolation. However, the effect of isolation on large islands is decreased by a 'target area effect' in that large islands receive more immigrants (Whitehead and Jones 1969). Furthermore, gene flow between source and island populations should be negatively correlated to isolation, leading to a higher probability of speciation on remote islands (Heaney 2000). Especially on large and heterogeneous islands, cladogenesis (in situ speciation; Stuessy et al. 2006) thus may counteract the negative effect of isolation on immigration (Heaney 2000, Losos and Schluter 2000, Kisel and Barraclough 2010).

Aside from isolation, area is the most fundamental parameter influencing island diversity patterns (Arrhenius 1921, Rosenzweig & Ziv 1999, Lomolino 2001) and can have both direct and indirect effects on species richness at three spatial levels (Connor & McCoy 1979). First, the direct effect at the regional level applies to the number of species that can coexist within a given region (MacArthur & Wilson 1967). It is still unclear, however, to which degree the increase of species numbers on larger islands is determined by the increase of area as such and by the associated increase in ecological carrying capacity, or by the larger number of habitats that are usually found on larger islands (Triantis et al. 2003, Kallimanis *et al.* 2008). Furthermore, species diversity is known to be dependent on spatial scale, with different factors having an impact at different scales (Levin, 1992; Whittaker, 2000; Whittaker et al., 2001). This also applies to the effect of area (Karger et al. 2011). Therefore, variables explaining species richness on a local spatial scale may not be the same as those accounting for richness at regional spatial scales (Willis & Whittaker 2002). At a regional scale, larger areas are well known to support more species, both because they maintain viable populations of more species and because they typically include higher habitat diversity (MacArthur & Wilson, 1967, Triantis et al., 2003). At the local scale, larger sampling areas typically include more species because they more completely sample the regional species pool (Connor & McCoy, 1979). However, even if sampling area is held constant, regional area will influence local species indirectly through the increase of the regional species pool ('echo pattern', sensu Rosenzweig & Ziv, 1999). Local communities can be perceived as a dynamic sample from the regional species pool (Terborgh 1973, Graves and Gotelli 1983, Cornell 1985, Ricklefs 1987) with the size of the surrounding area as a surrogate of the regional species pool (Terborgh and Faaborg 1980, Cornell and Lawton 1992, Caley and Schluter 1997, Cornell 1999, Romdal and Grytnes 2007). This 'echo pattern' has potential impact on the theory of island biogeography across spatial scales. If a strong 'echo pattern' is detectable on islands, then local

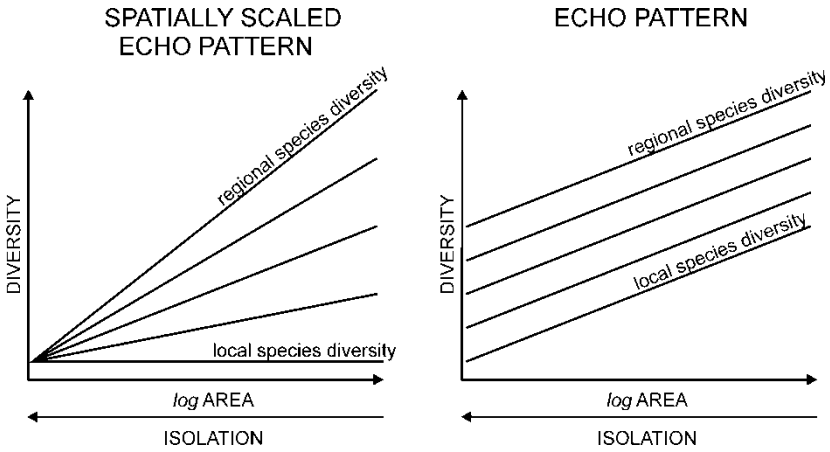

Figure 1 Hypothetical example how species richness changes with spatial scale in relation to island area and isolation. A scenario with a spatially scaled echo pattern on species diversity would lead to local scale diversity that does not change in accordance to island area (left). A scenario with a strong echo pattern will lead to a change in local species richness in accordance to the larger species pool on larger islands.

species diversity would increase with island area as the island species pool increases (Fig. 1). In contrast, if there is no 'echo pattern', or if it decreases at smaller spatial scales, local species diversity would show no change with island area at some point (Fig. 1). Clearly, a limited regional species pool will limit the number of species that can co-occur, but local richness may not increase continuously with increasing regional richness because at some point local communities may become saturated and α diversity remains constant (Huston 1999, Srivastava 1999). Consequently, local scale diversity would be determined by local environmental conditions limiting the number of individuals which can survive in a community, rather than biogeographical factors.

While several studies have investigated drivers of species richness at different scales (Rahbek and Graves 2001, Crawley and Harral 2001, Lennon et al 2001) an investigation on how well the theory of island biogeography performs on different spatial scales from plot to regional level has not yet been conducted.

We formulated two competing hypotheses in accordance with the above mentioned theoretical assumptions to address the question: Is the theory of island biogeography equally applicable at regional and local spatial scales?

H1: Area and isolation are important as predictors of species diversity at all spatial scales. The echo pattern will lead to an equal increase in diversity at all spatial scales. Therefore the equilibrium theory of island biogeography will be applicable at all spatial scales.

H2: Area and isolation are important as predictors of species diversity only at large spatial scales. The spatially scaled echo pattern affects local diversity depending on the spatial sampling scale. At local scales, diversity is entirely influenced by local environmental conditions while area and isolation lose their predictive power since communities are saturated. Therefore, the equilibrium theory of island biogeography will only be applicable at regional spatial scales.

To test if the theory of island biogeography is applicable at different spatial scales we selected twelve islands of different sizes in Indonesia and the Philippines and sampled fern diversity at six spatial scales. We tested if area and isolation are important predictors at all spatial scales of diversity or if local environmental conditions are more important than island biogeography at local spatial scales.

METHODS

Study sites

We selected 12 mountain regions on islands of different sizes, isolation and environmental conditions in Indonesia and the Philippines (Fig. 2). On each island, sampling sites were located at 1100 m and 1200 m within the main mountain range of the island (Table 1). We chose the altitude of 1100-1200 m because, on the one hand, this belt has a high number of fern and lycophyte (henceforth called fern) species (Bhattarai et al 2004, Carpenter 2005, Kluge & Kessler 2006, Kessler et al. 2011), enabling us to collect statistically relevant samples. On the other hand, human footprint in this elevation is the lowest worldwide (Nogués-Bravo 2008), providing us with mostly undisturbed natural ecosystems.

Table 1 Locations of the sampling sites in Indonesia and the Philippines.

Island	Mountain/Site	Latitude	Longitude
Luzon	Mingan Mountains	15°25'N	121°24'E
Sibuyan	Mt. Guiting Guiting	12°26'N	122°33'E
Panay	Mt. Madia-as	11°21N	122°08'E
Camiguin	Mt. Timpoong	09°11'N	124°42'E
Mindanao	Mt. Kitanglad	08°08'N	124°55'E
Mindanao	Mt. Hamiguitan	06°44'N	126°10'E
Sulawesi	Toro, Lore Lindu NP	01°29'S	120°03'E
Sulawesi	Gunung Duasudara	01°29'N	125°09'E
Tidore	Gunung Kiematubu	00°40'N	127°24'E
Bacan	Gunung Sibela	00°42'S	127°31'E
Buru	Wafehai	03°13'S	126°34'E
Seram	Manusela NP	02°59'S	129°11'E
Lombok	Gunung Rinjani	08°20'S	116°24'E
New Guinea	Pass Valley	03°46'S	139°14'E
New Guinea	Arfak Mountains	01°20'S	134° 8'E

Ferns as focal plant group

Ferns are distributed worldwide, and are independent of biotic pollination and distribution vectors because of their spore dispersal (Barrington 1993). The high species richness of ferns allows statistical inference of the documented data, and the relatively lower dependence from biotic vectors link patterns of distribution directly to abiotic factors.

Transect design

Samples were taken in standardized plots of 20 m x 20 m. This plot size has previously been used for surveys of local fern diversity (Kessler 2001, Kluge & Kessler 2006) and is large enough to be representative, but also small enough to be ecologically homogeneous and to allow rapid and efficient surveys (Kessler & Bach 1999). We used a fixed sampling design of four plots with a distance of 20 m. In each mountain range, two such transects were established at 1100 m and two at 1200 m (Fig. 2).

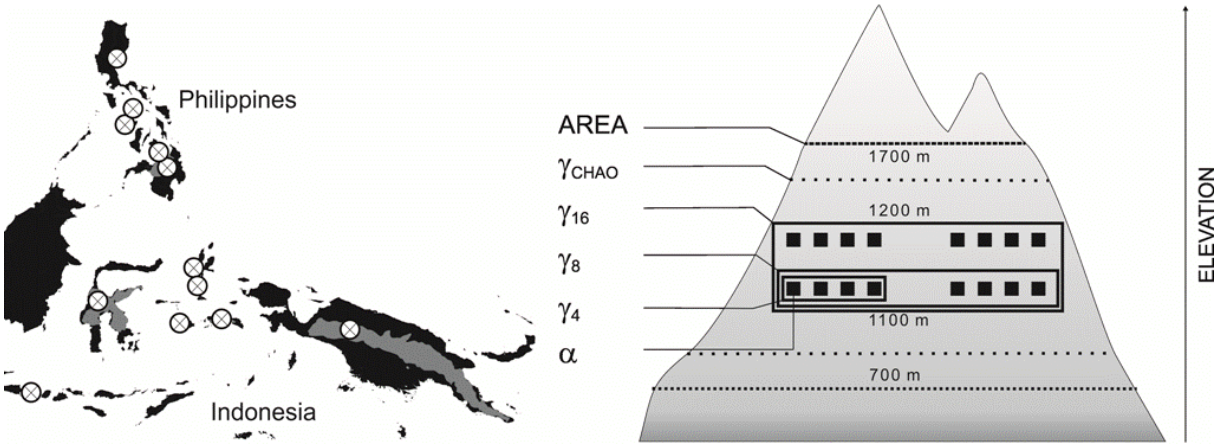

Figure 2 Sampling design. Left: Sampling locations (white circles with crosses) spanning the gradients of island area and isolation in the Malesian Archipelago and New Guinea. Right: Schematic representation of the sampling design consisting 16 plots of 20 x 20 m² each (mean richness = α) with one transect consisting four plots at fixed distances of 20 m (γ_4). Two transects of four plots each were arranged 100 m apart (γ_8), each at both 1100 m and 1200 m elevation (γ 16). γ_{CHAO} as an approximation of the local species pool was calculated using a species richness estimator (Chao 2) across all 16 plots. γ_{reg} is the species richness of the entire mountain range. AREA was measured as the land surface of each studied mountain range per island between 700 m and 1700 m a.s.l. (grey shades on islands, left).

Plant sampling

In each plot, we counted the number of fern species. Epiphytic species were surveyed by a combination of climbing on trees, cutting selected branches, looking for fallen branches on the ground, and through the use of binoculars. This approach has previously been successfully applied in studies of this kind (Kessler 2001, Kluge & Kessler 2006, Kessler et al. 2011). Every fern specie in each study region (but not in each plot) was collected for later determination and deposited in the Herbarium Zurich (ZH), Herbarium of the Central Mindanao University (Central Mindanao University Herbarium), Herbarium Bogor (BO), and the Herbarium University of California, Berkley (UC).

Data treatment

We defined α diversity as the mean richness per plot of 20 m x 20 m ($\alpha = \bar{S}$). γ_4 diversity was defined as the total number of species found in all 4 plots per transect, γ_8 diversity as the total number of species found in two transects for a total of 8 plots at a given elevation, and γ_{16} diversity as the total number of species found in four transects for a total of 16 plots. γ_{CHAO} diversity was calculated using the Chao 2 estimator (Chao 1984) based on γ_{16} diversity and the number of singletons and dobletons. γ_{reg} diversity was defined as the total number of fern species on an island quantified as the total number of species listed in the Flora Malesiana (Kalkman & Noteboom 1998).

Spatial scale

The term "scale" in this context refers to the size of the units used in the sampling of assemblages (Whittaker et al. 2001) and in our case ranges from 400 m² (α) to the whole mountain ranges (γ_{reg}; Fig. 1).

Explanatory variables

We used area, isolation, habitat heterogeneity, and bioclimatic and edaphic characteristics to explain species diversity at different spatial scales.

Area

As area, we defined the total habitat area within a mountain range where the sampling sites were located. For ferns, which have maximum diversity at mid elevations and few lowland species (Bhattarai et al. 2004), the lowlands are dispersal barriers for most species, rendering the mountain ranges the actual habitat islands. Using the whole surface area of an island would therefore be misleading. We calculated habitat area based on the total surface area of the elevational belt ranging from 700 m to 1700 m. This is the elevational range amplitude of the majority of montane fern species (Bhattarai 2004, Carpenter 2005, Kluge & Kessler 2006, Kessler et al. 2011) and allows an approximation of the area which hosts the species pool local communities are recruited from. We used ArcGis 10 (ESRI 2011) and SRTM topographic data at 90 m resolution (Jarvis et al. 2008) to calculate the surface area of the respective mountain ranges.

Isolation

Following Weigelt and Kreft (2012), we empirically chose a measure of island isolation varying the isolation component and the considered source landmass. Since the equilibrium model of island biogeography was formulated focussing on entire islands we selected the isolation metric based on the AIC of the linear model $\gamma_{reg} \sim$ Area + isolation considering only those models that showed the expected negative relationship among isolation and species richness. We found strongest support for the distance of each mountain range to the nearest mountain range of at least 100 km² on the mainland (Asia and Australia) as explanatory variable for fern species richness. Metrics considering the amount of mountain area in the surrounding of the mountain ranges did not show consistent relationships to richness at any spatial scale (see Appendix S1). We therefore used the distance to the nearest mountain range on the mainland of Asia or Australia as isolation metric.

Environmental variables

We used global temperature and precipitation models of nineteen different climatic variables derived from WorldClim – Bioclim (Hijmans et al. 2005) at a resolution of 30 arc-seconds. On a local scale ($\alpha - \gamma_{CHAO}$) data has been extracted for the location of the sampling plots. On the regional scale (γ_{reg}, γ_{CHAO}) we extracted the bioclimatic variables as the mean over the whole mountain range in which the sampling site was located.

Relative air humidity is a crucial environmental factor for ferns, but measuring it directly over long periods of time is not possible without considerable effort. Therefore, we used bryophyte cover on trees as proxy for relative air humidity following the methodology of Karger et al. (2012) which has been verified for five sites within the Philippines using data loggers for relative humidity. We also included local environmental factors such as mean inclination of the plot and canopy cover that were visually estimated in each plot. Soil samples were taken from every plot and analyzed for 15 different soil parameters (see Appendix S3).

Because the factors potentially covary and the use of more explanatory variables then observed variables violates the conditions for regression analysis, we reduced the environmental variables for regional climatic conditions (temperature and precipitation), as well as local environmental conditions using Principle Component Analysis (PCA). PCA axes were selected using a threshold of 70% variance explained (see Appendix S2). Where applicable, variables were standardized for zero mean unit variance to account for different measuring units.

Richness models

To test the applicability of the equilibrium model by MacArthur and Wilson (1967) at varying spatial scale, we compared the slopes of area and isolation as predictors of fern species richness from α to regional γ level. We used partial residuals to visualize the effect of each factor accounting for the respective covariable in linear multi-predictor models (S ~ A + I).

To account for regional differences in bioclimate and microclimatic, edaphic and structural conditions at plot level, we extended the models about axes derived from the bioclimate and plot-environment PCAs. The relative importance of each predictor in the multi-predictor framework was assessed using the pmvd metric in the R-package relaimpo (Groemping 2006).

RESULTS

The equilibrium model of MacArthur and Wilson applied best at regional level (Fig. 3, Table 2). The slopes of area increased with spatial grain and relationships were significant from the γ_{16} level upwards, both accounting for the effect of isolation and disregarding it. The slopes of the negative relationships between diversity and isolation decreased with increasing spatial grain. However, only at island level (γ_{reg}) was this relationship significant. The explanatory power of the equilibrium model measured as R^2 increased with the applied spatial grain (Table 2).

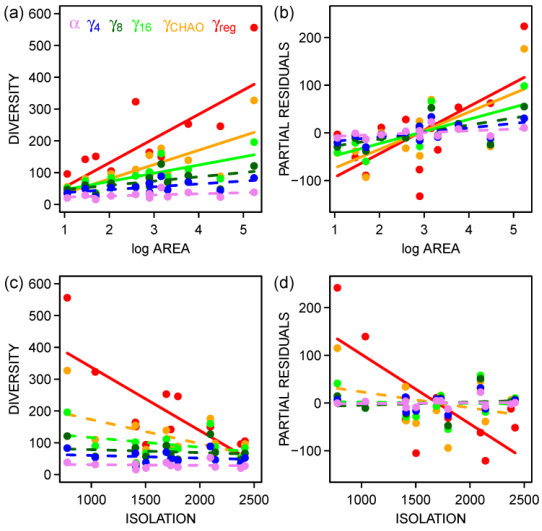

Figure 3 Diversity across different spatial scales plotted over area (a) and isolation (c) as well as partial residual plots accounting for the effect of the respective co-variable. Partial residuals are given for area (b) partialing out the effect of isolation and isolation (d) partialing out the effect of area. Spatial scales are colour-coded: α = pink, γ_4 = blue, γ_8 = dark green, γ_{16} = light green, γ_{CHAO} = orange, γ_{reg} = red. Regression lines are drawn using ordinary least square regression. Solid lines = significant ($p < 0.05$), dashed lines = not significant ($p > 0.05$).

Table 2 Model statistics for area and isolation as descriptors of diversity at different spatial scales. est. = estimated values.

	Intercept			Area			Isolation			R^2
response	est.	t	p	est.	t	p	est.	t	p	
γ_{reg}	303.6	2.388	0.041	49.4	2.365	0.042	-0.1	-2.879	0.018	0.74
γ_{CHAO}	64.2	0.698	0.503	39.1	2.585	0.029	0	-0.911	0.386	0.57
γ_{16}	26.6	0.468	0.651	25.4	2.723	0.023	0	-0.125	0.903	0.52
γ_8	18.3	0.418	0.686	14.7	2.049	0.071	0	0.377	0.715	0.34
γ_4	24.2	0.825	0.431	9.39	1.945	0.084	0	0.151	0.883	0.33
α	15.3	0.893	0.395	3.8	1.349	0.21	0	0.283	0.783	0.18

The relative importance of area decreased with the spatial grain of the units at which diversity was measured (Table 3). Only when diversity was measured as the diversity of the entire island (γ_{reg}), relative importance of area was lower than expected from the linear decrease (?). The pattern of isolation as predictor of fern species richness was less pronounced (Table 3). However, a decrease of relative importance from regional and Chao diversity to plot level diversity was apparent. Temperature did not explain diversity at any given grain level (Table 3). Regional precipitation ($PRECPC2_{reg}$) was only important at regional level but not at grains smaller than γ_{CHAO} (Table 3). Local environmental conditions (ECOPC3) showed a clear increase in relative importance with decreasing spatial grain (Table 3). Maximum relative importance of environmental conditions was found at the γ_4 level (Table 3).

Table 3 Relative variable importance of explanatory variables for the different spatial scales. AREA = area of the mountain range, Temp = Temperature PCA, Prec = precipitation PCA, ECOPC3 = local environmental conditions PCA axis 3.

	γ_{reg}	γ_{CHAO}	γ_{16}	γ_8	γ_4	α
AREA	0.2	0.3	0.3	0.2	0.1	0
Isolation	0.4	0.1	0	0	0	0
$TEMP_{Reg}$	0	0	-	-	-	-
$PRECPC1_{reg}$	0	0	-	-	-	-
$PRECPC2_{reg}$	0.2	0.2	-	-	-	-
TEMP	-	0	0	0	0	0
PREC	-	0	0	0	0	0
ECOPC3	-	0.2	0.4	0.4	0.6	0.6

DISCUSSION

At the regional scale (γ_{reg}), we found the expected relationships of species richness per mountain range to both area and isolation, as predicted by the classical theory of island biogeography (MacArthur and Wilson 1967, Whittaker 1998). On the other hand, the marked decline in importance of area and isolation at smaller spatial scales shows that the theory of island biogeography loses its predictive power with decreasing spatial scale from regional to plot level (Fig. 3). This decline was most pronounced on large and isolated islands.

At the most narrow (α) scales, however, diversity was neither correlated with area nor isolation. Based on these results we have to reject our hypothesis that the echo pattern has equal influence across spatial scales (H1) in favour of a spatially scaled echo pattern on islands (H2). The theory of island biogeography is therefore not applicable at small spatial scales, but has some predictive power at intermediate scales. This leads us to conclude that the influence of the species pool on local diversity is scale dependent and decreases with decreasing spatial scale. A possible explanation for this pattern could be that local (α) diversity is saturated and diversity becomes less saturated at larger scales. A local community is considered saturated when the maximum number of species that can disperse into the community, find a suitable niche and keep a viable population size, is reached (Fox & Srivastava 2006). In addition, a community can be saturated simply because the upper limit of species richness is reached due to ecological constrains (Srivastava 1999). The strong increase in the importance of environmental factors with decreasing

spatial scale would favour these assumptions (Table 3). At the α scale, species diversity thus can be considered to be saturated since the maximum fern diversity possible under the current environmental conditions appears to have been reached. Therefore, an increase in the species pool can have no effect on local species diversity, since the maximum number of species that the local assemblages can hold has been reached.

Temperature did not show any relation to species diversity at any scale (Table 3). Considering that all of our investigated islands are within the tropics without a pronounced temperature gradient this is not surprising for temperature. Precipitation, however, seems to be important for diversity at regional and intermediate scales (γ_{reg}, γ_{CHAO}). This regional influence of precipitation on fern diversity has been shown before on a macroecological scale (Kreft et al. 2010). Its importance however, declines towards smaller scales and local environmental factors become more important (Table 3).

Isolation did not show the same pronounced patterns as area across spatial scales. Although a decline in the importance of isolation was detectable to some degree (Fig. 3), declines in species richness due to isolation are only marginally significant. In fact, only few of the tested isolation metrics showed a significant effect, and only at the largest scale (γ_{reg}) (see Appendix S1). This might be partly due to the relatively small sampling size of twelve islands, but most likely reflects the fact that the variability of isolation among our study islands was much less than that of area. In addition, the comparatively low importance of isolation might also be linked to a higher degree of cladogenesis on large islands which may counteract the negative effect of isolation on species richness, especially on large islands such as New Guinea or Mindanao (Heaney 2000, Kisel and Barraclough 2010, Weigelt & Kreft 2012).

In conclusion, we found that the two main components of the theory of island biogeography, area and isolation, are good predictors of fern diversity on islands at regional scales. The species pool has a scale dependent influence on diversity (a spatially scaled echo pattern) and is unimportant at the local (α) scale where diversity appears to be saturated. At this scale, local environmental conditions become far better predictors of fern diversity. The lack of explanatory power of area at the local α scale is most likely due to the species saturation of communities at this spatial scale. To make predictions about diversity on islands it is therefore important to take the scale dependence of species pool effects into account and acknowledge that they only predict species diversity up to the scale at which diversity becomes saturated.

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BIOSCETCHES

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Author contributions: D.N.K, P.W. and M.K. conceived the ideas; D.N.K., V.B.A., A.H., D.D. and M.K. collected the data; D.N.K and P.W. analysed the data; and D.N.K., P.W., M.K. and H.K. led the writing.

SUPPLEMENTARY MATERIAL

Appendix S1 Isolation metrics tested as predictors of regional fern diversity. Estimates and AIC values are derived from a linear regression model with habitat area and one isolation metric at a time as predictors of fern species richness. Note that metrics quantifying the proportion of mountain area in the surrounding of the target mountain range increase with decreasing isolation. Significance of parameter estimates: * $p < 0.05$, ** $p < 0.01$. The metric chosen for the analyses is printed in bold. Of all metrics showing the expected negative relationship of isolation to richness it has the lowest AIC value.

Isolation metric		**Estimate**	**AIC**
Source landmass description	Area / Buffer		
Distance to nearest mountain range (> 700 m a.s.l.) of certain minimum area	100 km²	-0.19	150.4
	1000 km²	-0.43	147.5
	10000 km²	-0.23 *	144.6
	100000 km²	0.08 *	142.5
	1000000 km²	-0.02	150.2
Distance to nearest mountain range (> 700 m a.s.l.) of certain minimum area on a different island than the target mountain range	100 km²	-0.22	150.2
	1000 km²	0.09	150.3
	10000 km²	0.31 *	144.4
	100000 km²	0.08 *	142.5
	1000000 km²	-0.02	150.2
Distance to nearest mountain range (> 700 m a.s.l.) of a least 100 km² on landmass of certain minimum area	100 km²	-0.19	150.3
	1000 km²	0.24	149.5
	10000 km²	0.28 **	140.7
	100000 km²	0.27 *	143.8
	750000 km²	0.01	150.4
	1000000 km²	**-0.15 ***	**142.6**
	10000000 km²	0	150.5
Distance to nearest mountain range (> 700 m a.s.l.) of a least 100 km² on New Guinea	-	0	150.5
Proportion of mountain area (> 700 m a.s.l.) within a certain buffer distance in the surrounding of the target mountain range	10 km	-1817.78	149.3
	32 km	451.06	150.2
	100 km	1277.74	147.3
	316 km	2367.94	147.7
	1000 km	-7426.26 *	143.2
	3162 km	1332.25	148
Proportions combined: log10 (∑ proportion)	-	554.24	149.1

Appendix S2 Eigenvalues and cumulative proportion explained (cum. prop. expl. [%]) for variable reduction using principal component analysis (PCA). Only axis used in the analysis are shown.

Variable Set		**PC1**	**PC2**	**PC3**	**PC4**
Temperature local	eigenvalue	338800	-	-	-
(TEMP)	cum. prop. expl.	0.73	-	-	-
Precipitation local	eigenvalue	32730	-	-	-
(PREC)	cum. prop. expl.	0.90	-	-	-
Temperature regional	eigenvalue	35440	-	-	-
($TEMP_{Reg}$)	cum. prop. expl.	0.95	-	-	-
Precipitation regional	eigenvalue	173700	73890	-	-
($PREC_{Reg}$)	cum. prop. expl.	0.63	0.90	-	-
local Ecology	eigenvalue	5.264	4.0373	1.9853	-
(ECO)	cum. prop. expl.	0.35	0.62	0.75	-

Appendix S3 Explanatory factors used in the analysis of diversity along the island size gradient.

Explanatory factor
log Habitat area [km²]
Isolation [km]
Precipitation [PCA]
Temperature [PCA]
Bryophyte cover on trees [%]
Variation in Bryophyte cover on trees [%]
Mean Inclination [°]
Canopy cover [%]
Soil carbon content [mmol/g]
Soil nitrogen content [mmol/g]
Carbon/nitrogen ratio
Base saturation [%]
Nitrogen ion content [µmolc/g]
Aluminium ion content [µmolc/g]
Calcium ion content [µmolc/g]
Iron ion content [µmolc/g]
Kalium ion content [µmolc/g]
Magnesium ion content [µmolc/g]
Manganese ion content [µmolc/g]
Natrium ion content [µmolc/g]

Chapter 4

Bryophyte cover on trees as proxy for relative air humidity in the tropics

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Short communication

Bryophyte cover on trees as proxy for air humidity in the tropics

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ABSTRACT

Climatic conditions are a prime candidate to explain local patterns of biodiversity and consequently there is great need of on-site climatic measurements. Among them, however, air humidity is notoriously difficult and time-consuming to measure, and it has been proposed that the epiphytic bryophyte cover can be used as an indicator of long-term air humidity conditions. Here we explore the utility of visually estimated epiphytic bryophyte cover on large canopy branches as a proxy for air humidity at 26 study sites in tropical forests where we measured microclimate for at least 12 months. Across all sites, bryophyte cover was weakly related to relative air humidity (R^2 = 0.17), but when we separated highland (1800–3500 m elevation) from lowland (<1800 m) sites, relative air humidity showed significant and distinct relations to bryophyte cover (R^2 = 0.36–0.62), whereas temperature was related to bryophyte cover only in the lowlands (R^2 = 0.36). We conclude that epiphytic bryophyte cover can be used as a proxy for air humidity if temperature and elevation are taken into account within a circumscribed study region, but might not be applicable for comparisons across extensive elevational gradients or wide differences in temperature.

1. Introduction

Air humidity plays a central role in determination of plant morphology and physiology (via control of transpiration) and consequently for plant productivity (e.g., Kozlowski and Pallardy, 1997; Lendzion and Leuschner, 2009; Leuschner, 2002). Accordingly, air humidity is commonly considered to be crucial in influencing the distribution of species and the structuring of plant communities (Lendzion and Leuschner, 2009; Leuschner and Lendzion, 2009). Despite this ecological importance, quantitative data on air humidity are often hard to obtain, especially in tropical regions. Air humidity cannot be derived from climate models and its measurement in the field requires considerable effort. For these reasons, measures of air humidity are often limited to short time periods or few localities, restricting the inclusion of this important factor in many ecological studies. Therefore, estimating the bryophyte cover on trees as a proxy for air humidity has become increasingly popular in ecological studies (e.g., Frahm and Gradstein, 1991; Kessler et al., 2011; Kluge et al., 2006; Wolf, 1993).

While the relation between air humidity and bryophyte cover is intuitively appealing and supported by observational reports (Gehrig Downie et al., 2011; Kluge et al., 2006; Obregon et al., 2009; Sporn et al., 2009; Wolf, 1993), a quantitative study on this relationship is still lacking. In humid tropical forests bryophytes are most abundant at high elevations in mountains above the level of cloud formation, where air humidity is generally high (Frahm and Gradstein, 1991), int contrast they are almost absent on lowland trees, except in valleys with early morning fog accumulation (Gehrig Downie et al., 2011; Obregon et al., 2009). Various explanations have been suggested for these patterns. One relates to the fact that bryophytes are poikilohydric, i.e., they are unable to balance their water potential on their own (León Vargas et al., 2006; Sporn et al., 2009). Therefore, air humidity has a direct effect on bryophytes by stopping their photosynthesis below approximately 95% relative air humidity (RH) (León Vargas et al., 2006). Low levels of air humidity can, however, be easily tolerated by bryophytes due to their desiccation tolerance. After remaining dormant during periods of low air humidity, they can return to their normal metabolism within a few hours (Proctor et al., 2007). Alternatively, it has been suggested that high temperatures limit the growth of bryophytes due to elevated respiration rates, especially during the night when there is no photosynthetic activity (Frahm, 1990a, 1990b; Zotz et al., 1996). Furthermore, the survival rate of desiccated bryophytes declines steeply with increasing temperatures, limiting the ability to recover from periods of low air humidity (Proctor, 1984).

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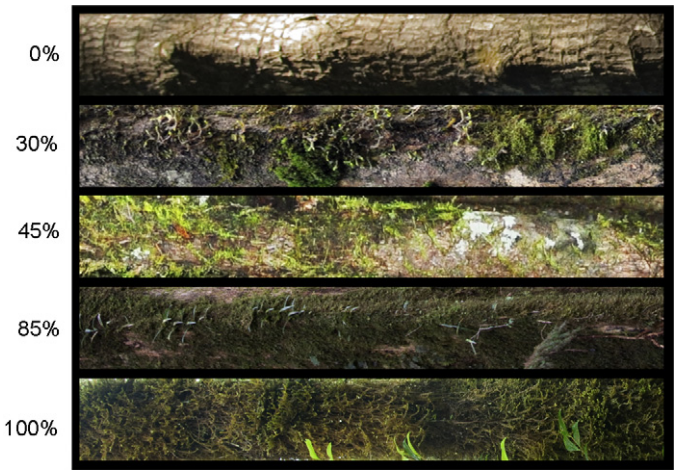

Fig. 1. Examples of estimates of bryophyte cover on trees in tropical forests. The percentage reefers to the area covered by bryophytes in relation to the whole area. To estimate the bryophyte cover in a 20 m × 20 m plot, the whole area of all branches within the plot was used.

In the present study, assess the performance of epiphytic bryophyte cover as proxy for air humidity using microclimatic data recorded over the last decade in a series of field studies at 26 tropical forest sites.

2. Material and methods

2.1. Data acquisition

Climatic variables (air temperature, RH) were measured using Hobo Pro v2 temp/RH and Hobo Pro temp/RH data loggers (Onset Corp., MA, USA) at 14 sites in Ecuador, 6 in Costa Rica, and 6 in the Philippines at different elevations ranging from 40 m to 3500 m above sea level (Table 1). Data loggers were placed at 1.5–2 m height in the forest understorey for a measuring period of at least 12 months. Measuring interval was 1 h.

Bryophyte cover was estimated visually by assessing the mean percentage of bryophyte cover on all larger canopy branches (minimum size: 5 cm branch diameter) of all trees within a plot of 20 m × 20 m surrounding the sites of the placement of the data loggers. As measure for the bryophyte cover, the percentage of area covered with bryophytes in relation to the uncovered area was used (Fig. 1). If necessary, binoculars were used to estimate bryophyte cover and to distinguish between bryophytes and vascular epiphytes. Canopy branches were used to estimate bryophyte cover, because bryophyte cover in the forest understorey is generally sparse and does not vary as conspicuously as in the canopy (Frahm and Gradstein, 1991; Wolf, 1993). On the other hand, we did not place the data loggers in the canopy due to problems of accessibility. However, at one of our locations (Costa Rica), we measured RH both in the understorey and in the canopy and found that both were strongly correlated across elevational and habitat gradients (6 plots, mean correlation $r = 0.92$, range $r = 0.83$–0.96, $p \leq 0.001$ across all plots) (Fig. A.1), although RH tended to decrease more pronouncedly during sunny weather in the canopy.

2.2. Data analysis

Aside from air temperature and relative humidity we also incorporated the vapour pressure deficit (VPD), which was calculated using the Magnus equation (Magnus, 1844):

$$\mathrm{VPD} = e - ea\,[\mathrm{kPa}] \quad (1)$$

with

$$e = 0.6108 \times \exp\left(17.27 \times \frac{T\,[^{\circ}\mathrm{C}]}{T\,[^{\circ}\mathrm{C}] + 237.3}\right) \quad (2)$$

León Vargas et al. (2006) stated that mean annual values are of little significance in determining bryophyte distribution. Therefore, we used 28 different approaches to determine the influence of air temperature and air humidity on bryophyte cover. The basic parameters considered were elevation above sea level, mean daily temperature, mean daily RH, mean daily VPD, minimum daily temperature, minimum daily RH, maximum daily temperature, and maximum daily VPD. Because it has previously been recognized that high night time temperatures influence bryophyte physiology due to high respiration (Frahm, 1990a, 1990b; Zotz et al., 1996), we further conducted all measurements mentioned above separately for daylight hours and night times. Aside from these measurements, we also assessed the potential influence of mean daily maximum temperature, mean daily minimum RH, and mean daily maximum VPD which also could be potential limiting factors for bryophyte growth. In addition, we calculated the number of days per year in which the mean RH dropped below 95%, and in which the minimum RH dropped below 95%, to identify how many days per year the bryophytes experienced water stress. To check for an influence of the length of dry periods, we calculated the mean length of dry periods (given by the hours < 95% RH/year).

We used linear regression analysis to access the effects of the climate variables on bryophyte cover. Additionally, we performed a Mixed Effects Linear Model with locality and elevation as random factors controlling for observer bias, local environmental conditions and time inconsistencies. Elevational level was included to take into account possible differences between lowland and highland forests. Since the boundary between these two levels is rather arbitrary and varies from one site to another (Frahm and Gradstein, 1991; Kessler, 2000), we considered all sites above 1500 m asl as highlands. At this elevation, cloud condensation regularly occurs at all our study locations. All analyses were conducted using R (R Development Core Team, 2011) and the package "nlme" (Pinheiro et al., 2011).

3. Results

The different measures of air humidity and temperature all yielded qualitatively identical results. For the sake of clarity we only report here in detail on the mean annual RH and temperature values, but this does not imply that we believe that these variables may be ecologically more important than others. Data on the other variables can be found in the supplementary materials (Table A.1 and Fig. A.2).

RH showed a barely significant relationship with bryophyte cover for all study sites and all measured humidity variables (Fig. 2), VPD also only showed a weak relationship with bryophyte cover (Table A.1). Maximum temperature during the night, during daylight and within 24 h, showed moderate relationships with bryophyte cover. When we considered lowland and highland sites separately, RH and VPD showed strong relationships with bryophyte cover both in the lowlands and the highlands whereas mean annual temperature showed only a significant relationship with bryophyte cover in the lowlands and maximum temperature only in the highlands (Fig. 2, Table A.1). For lowland sites, minimum daily RH showed the highest relationship with bryophyte cover ($R^2 = 0.80$, $p < 0.001$), whereas in the highlands mean daily VPD and mean VPD during daylight (both: $R^2 = 0.76$, $p < 0.001$) showed the highest relationships (Table A.1).

The Mixed Effects Linear Model, taking locality as random factor into account, also showed significant relationships of bryophyte cover to mean annual RH and temperature (Table 2). There was

Table 1
Data sources and detailed description of the surveyed locations. Bryophyte cover estimation has been conducted at the beginning of the time period measured.

Location	Elevation	Time period measured	Forest type	Coordinates	Source
Costa Rica					Kluge et al., 2006
La Selva	40 m	24.07.2002–23.07.2003	Lowland rainforest	N10°25′36.12″ W84°0′42.84″	
Ceibo	650 m	24.07.2002–23.07.2003	Lowland rainforest, border zone to lower montane rainforest	N10°18′46.08″ W84°4′26.04″	
San Rafael (3 Plots)	1800 m	24.07.2002–23.07.2003	Lower montane rainforest	N10°12′12.6″ W84°5′35.88″	
Barva	2800 m	24.07.2002–23.07.2003	Upper montane rainforest	N10°8′9.24″ W84°6′21.6″	
Ecuador					Unpubl. data
San Francisco	2545 m	01.11.2004–30.10.2005	Upper montane rainforest, Purdiaea	S03°59′28″ W79°04′15″	
San Francisco	2455 m	01.11.2004–30.10.2005	Upper montane rainforest, Purdiaea	S03°59′23.0″ W79°04′20.8″	
San Francisco	2500 m	01.11.2004–30.10.2005	Upper montane rainforest, Purdiaea	S03°59′33.6″ W79°04′14.5″	
Tapichalca	2550 m	01.11.2004–30.10.2005	Upper montane rainforesT	S4°29′1.2″ W79°8′16.2″	
Tapichalca	2650 m	01.11.2004–30.10.2005	Upper montane rainforest	S4°29′21″ W79°7′4.8″	
Tapichalca	2650 m	01.11.2004–30.10.2005	upper montane rainforest	S4°29′21″ W79°7′4.8″	
Tapichalca	2400 m	01.11.2004–30.10.2005	Upper montane rainforest	S4°29′21″ W79°7′4.8″	
El Tiro	2575 m	01.11.2004–30.10.2005	upper montane rainforest	S3°59′22.2″ W79°7′47.4″	
Jatun Sacha	500 m	13.04.2010–12.04.2011	Lowland rainforest	S1°4′2.28″ W77°37′0.12″	
Jatun Sacha	1000 m	13.04.2010–12.04.2011	Pre-montane rainforest	S0°48′51.84″ W77°34′39.36″	
Cordillera Galeras	1500 m	13.04.2010–12.04.2011	Lower montane rainforest	S0°49′40.08″ W77°32′21.12″	
Cordillera Guacamayos	2000 m	13.04.2010–12.04.2011	Upper montane rainforest	S0°38′17.88″ W77°50′23.64″	
Yanayacu	2500 m	13.04.2010–12.04.2011	Upper montane rainforest	S0°35′22.92″ W77°53′53.88″	
Oyachachi	3500 m	13.04.2010–12.04.2011	Upper montane rainforest,	S0°11′35.88″ W78°7′35.04″	
Philippines					Unpubl. data
Luzon, Mingan Mountains	1100 m, 1200 m	29.10.2009–28.10.2010	Lower montane rainforest	N15°25′31.15″ E121°24′18.16″	
Mindanao, Mt. Kitanglad	1200 m	29.10.2009–28.10.2010	Lower montane rainforest	N8°8′37.63″ E124°55′9.26″	
Mindanao, Mt. Hamiguitan	1100 m, 1200 m	29.10.2009–28.10.2010	Lower montane rainforest	N6°44′9.41″ E126°10′1.51″	
Camiguin, Mt. Timpoong	1200 m	29.10.2009–28.10.2010	Lower montane rainforest	N9°11′1.73″ E124°42′56.30″	

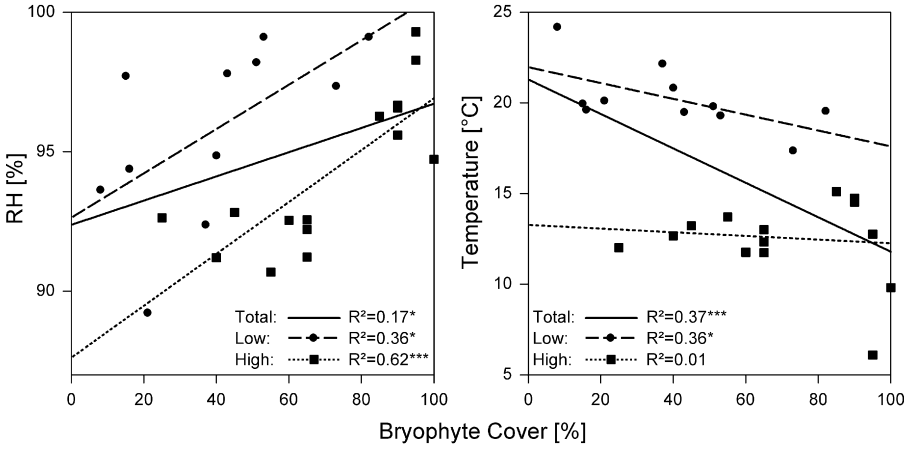

Fig. 2. Relationship of visually estimated bryophyte cover on canopy tree branches with mean annual relative air humidity (RH) and mean annual temperature at 26 sample sites in tropical forests. The solid lines represent the linear fit for the entire dataset (Total), the dashed lines (circles) the fit for the lowland sites (Low) only and the dotted lines (squares) that for the highland sites (High) only (significance codes: $^{*}p < 0.05$, $^{***}p < 0.001$).

Table 2
Mixed effects linear model relating visually estimated bryophyte cover on canopy tree branches to mean annual temperature and mean annual relative air humidity, with Locality as random factor.

	Df	Sum Sq	Mean Sq	*F* value	p
Mean RH	1	3096.3	3096.3	16.7945	<0.001
Mean temp	1	4496.7	4496.7	24.3899	<0.001
Mean RH:mean temp	1	1177.0	1177.0	6.3842	<0.05
Residuals	19	3503.0	184.4		

a slightly significant interaction between mean annual temperature and mean annual RH but both variables were not significantly correlated, neither across the entire dataset ($r = 0.12$, $p = 0.55$) nor when lowland ($r = 0.48$, $p = 0.13$) and highland ($r = 0.13$, $p = 0.66$) sites were separated. The Mixed Effects Linear Models using elevational level as random factor to test for differences in the intercept of the two models showed a significant difference of 5.6% RH in the intercept of both models ($p < 0.001$), with the highland sites having the lower intercept.

4. Discussion

Our study confirms the intuitively appealing relationship of bryophyte cover on canopy branches and RH, as predicted e.g., by Frahm and Gradstein (1991), Gehrig Downie et al. (2011), Kluge et al. (2006), Obregon et al. (2009), Sporn et al. (2009), and Wolf (1993). It also suggests that the visual estimation of bryophyte cover on branches can be used as a proxy for air humidity when detailed measurements are unfeasible. While the visual estimation may appear to be a rough, non-quantitative method, we consider that it is superior to almost any quantitative approach because of the high spatial variability of bryophyte cover in the tree canopy, with differences between tree species, tree individuals, different positions in the crown as well as in relation to branch diameter, inclination, and age (Wolf, 1993; Gehrig Downie et al., 2011). To adequately sample this variability by climbing into the tree crowns to collect samples would require dozens if not hundreds of individual samples which is too time consuming to be useful as a proxy method. In such a situation, a visual estimation can average and integrate this variability. The only caveat with this method is observer bias and we suggest that within a study estimates should always be performed by the same person.

We found that different measures of air humidity involving both RH as well as VPD showed similar patterns which is unsurprising because the calculation of VPD is mainly based on RH and both factors are strongly correlated ($r = -0.95$, $p < 0.001$). Our study is therefore unsuitable to discern which aspect of air humidity, e.g., mean values against maxima or minima, is ecological more meaningful. Disentangling this situation will require detailed ecophysiological studies. In the following, we therefore talk about air humidity in general, without any assumption as to which individual factors may be crucial.

Perhaps the most important result of our study is that the relationship between bryophyte cover and air humidity was only evident when we separated the data by elevational levels. Same bryophyte covers in lowland sites on average showed ca. 5.6% higher mean annual RH than highland sites (Fig. 2). In addition, mean annual temperature showed a significant relationship with bryophyte cover only in the lowlands and maximum temperature only in the highlands. While ecophysiological studies are needed to confirm our conclusions, we interpret these results as follows. We believe that while air humidity influences bryophyte growth everywhere, in the lowlands high temperatures pose an additional stress factor by increasing desiccation even at high levels of air humidity and by increasing nocturnal respiration (Frahm, 1990a, 1990b; Zotz et al., 1996). Accordingly, higher levels of air humidity are required to obtain similar levels of bryophyte cover in the lowlands than in the highlands. In the highlands, low temperatures are likely to be a limiting factor for plant growth. Short times of high temperatures therefore may have a positive effect of bryophyte growth by promoting plant growth as long as high humidity is sustained.

We further found that measurements of air humidity considering only diurnal values showed higher correlations with bryophyte cover than nocturnal values. This suggests that air humidity has a stronger effect on bryophyte growth when the plants are photosynthetically active than during the night when they are dormant.

Overall, determination coefficients of RH and VPD (R^2 values) were reasonably high (0.36–0.80), showing that much variation of bryophyte cover could be accounted for by air humidity. Other factors might play a role here, for example the fact that bryophyte cover was estimated by different people, or differences in vegetation structure. The data was collected during different years at the different locations, and climatic anomalies like the El Niño effect might have altered the observed pattern to some degree. In any case, this effect would be taken into account by our mixed effects model, in with locality–and hence measurement year–as a random factor. But even taking these effects into account, relative humidity and temperature still showed a significant impact on the bryophyte cover. Another factor, especially in the highlands, might be that our estimation of bryophyte cover only took into account the branch surface area covered by bryophytes, but not the thickness of the bryophyte layer or pendulous live forms, which can be quite abundant at high elevations (León Vargas et al., 2006). Therefore, total bryophyte biomass might be strikingly different especially at high levels of bryophyte cover (>90%) when pendulous life forms are present and when liverworts have grown into thick carpets (Mandl et al., 2010; Wolf, 1993).

5. Conclusions

Bryophyte cover can be used as a reasonably reliable proxy for air humidity for studies, where levels of air humidity vary considerably, where approximate assessments of air humidity are sufficient, and where microclimatic measurements cannot be conducted due to financial or logistical limitations. We caution against comparing bryophyte cover estimates across extensive elevational gradients, between different geographical regions, and obtained by different field workers. We finally suggest that the estimation approach might be improved by including estimates of the thickness of bryophyte mats and the abundance of pendulous bryophytes.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolind.2012.02.026.

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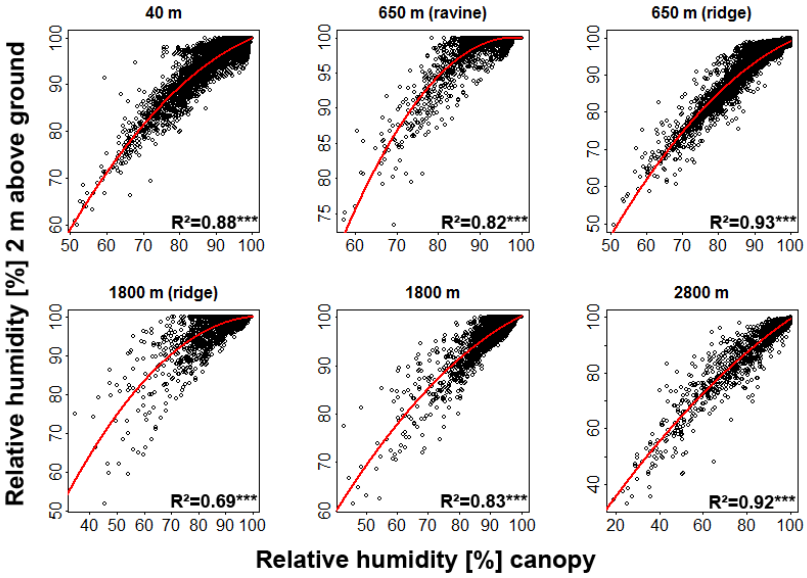
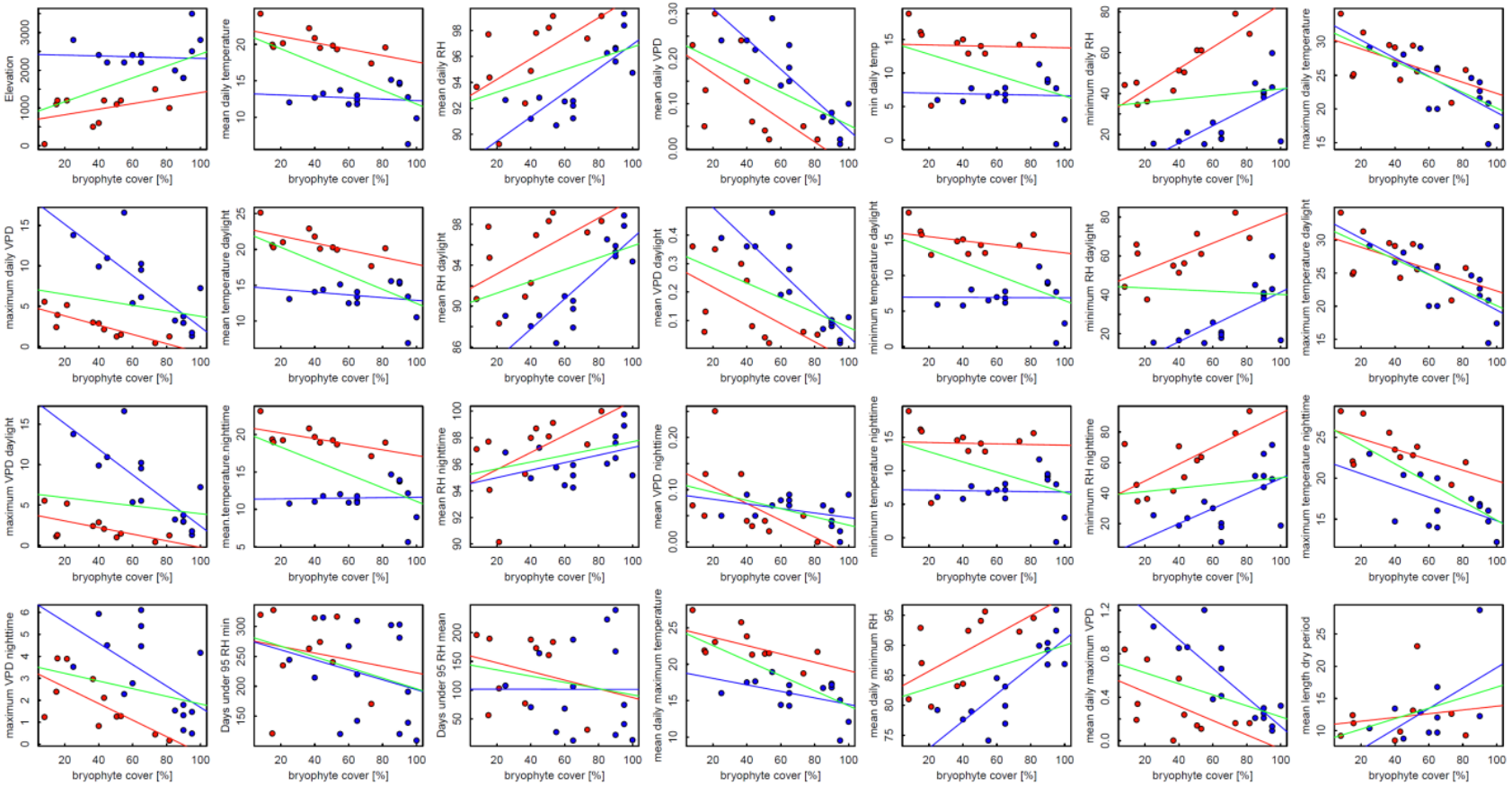
APPENDIX



SUPPLEMENT 1. Relationship of relative humidity [%] measured 2m above the ground with relative humidity [%] measured in the canopy at four different elevations. Ravine refeers to measuring site located in a ravine within the forest, ridge to a measuring site located at a ridge of the mountain. Red lines show the quadratic regression. $p<0.05$*,$p<0.01$**,$p<0.001$***.



SUPPLEMENT 2. Different measurements of relative humidity and temperature in comparison to bryophyte cover.

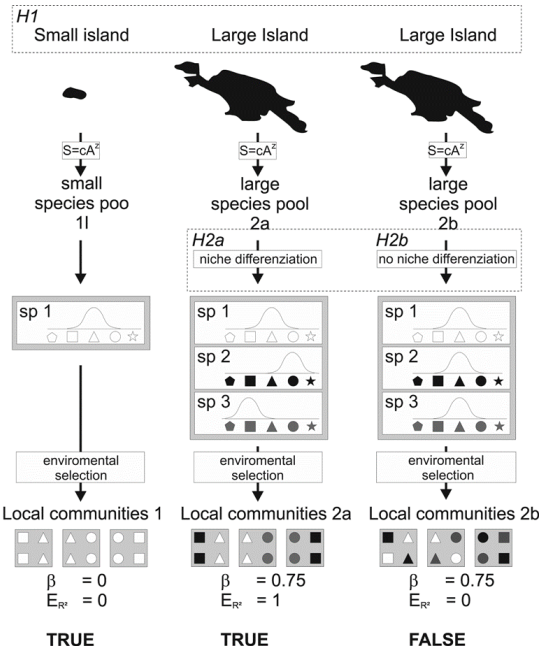
CONCLUDING REMARKS

The questions answered in this thesis led me to a set of conclusions of how species diversity is determined across spatial scales. The answers to these specific questions however, raised new questions which need to be answered in the future to understand better: What determines species diversity?

The first conclusion of **Chapter 1**, that: "regional surface area seems to be largely responsible for the differences between local and regional species richness patterns along elevational gradients", lead me to the question, "What aspect of area is responsible for the difference between local and regional diversity along elevational gradients?" Is it only the sampling effect - a higher area sampled includes more species? Is it habitat heterogeneity? Is it the species pool?

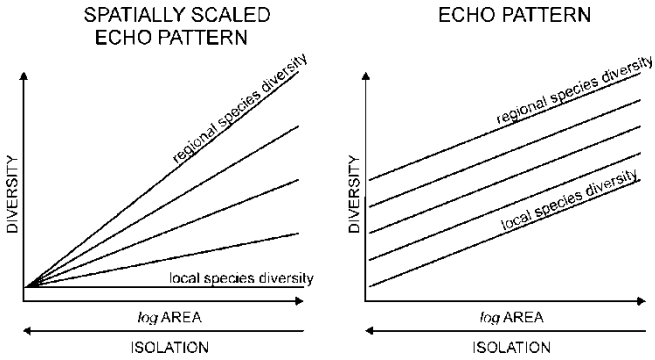
The second conclusion of Chapter 1, that: "…if area is indeed the only factor important in the difference between local and regional elevational richness patterns, then the similarity between the two patterns may be taken as an indication that both are reflections of one general pattern driven by a common suite of underlying processes, rather than by different processes at different spatial scales." A conclusion which I realized later on is only partly true. The conclusion of Chapter 3 shows that the echo pattern, the influence of the species pool on local communities, is scale dependent.

The paper got published in 2011, with the first manuscript submitted in late 2009. Since then my view of how species diversity is influenced across spatial scale has evolved. One question which arose from the study after publication corresponds to the slope of the species area relationship (z-value) which I used to correct regional richness for area. Is it really the same for all elevational belts? It does not seem to matter much for the conclusion that area is responsible for the difference of regional and local diversity in this case; it rather shows that the z-value seems to be a key component in how area influences regional richness. The z-value is a representation of how fast species diversity changes with an increase in area, a phenomenon which can also be measured using indices for β diversity. Might measuring β diversity at every given elevation help us to understand better in what way regional diversity is linked to local diversity?



The conclusion of **Chapter 2** is in my opinion the key outcome of this thesis. It gives a neat and simple explanation of how local communities are influenced by the species pool and what mechanisms are behind it (Fig C1). For me it carries two important messages regarding species diversity across scales. First, the species pool influences local community composition thru increasing competition. As immigration from the species pool increases due to a larger species pool, competition increases. Second, it shows that species communities are not "neutral". A question which came up several times while presenting the research for the first time at the IBS meeting in Miami in 2013: "Could you

imagine if the patterns observed could also be possible with a 'neutral' community?" "No, it would be not!", as I hope I can show in Figure 6, Chapter 2 (previous page). Some scientists might challenge my conclusion, but to cite ROBERT E. RICKLEFS ON the matter: "The fact that intelligent people can seriously consider a theory of biodiversity that contains no ecology – I am referring to Stephen Hubbel's 'neutral theory'…should cause us to reconsider what we know." (Ricklefs 2011).



The conclusion of **Chapter 3** shows how important it is to consider spatial scale when we design theories explaining species diversity. It also shows in a compelling way what mechanisms are responsible for a theory to be applicable on one scale, but loses its predictability on others. It was surprising for me to find that the echo pattern is scale dependent rather than continuous throughout spatial scale. I have to admit, when starting the fieldwork in the Philippines; I would have bet a lot on a continuous influence of regional diversity on local diversity. However, visiting the fourth sampling site - Camiguin Island a small island just north of Mindanao, I started to question this initial assumption. The alpha diversity on this small island was almost as high as that of the fifty times larger island of Panay. Sampling more and more islands, the scale dependence of the echo pattern became more apparent. Coming to that conclusion it shows me how important it is to show this scale dependence, since I believe I am not the only one who shares my initial belief of a continuous echo pattern.

The conclusion of **Chapter 4** is not exciting for me at all. "*Where it's humid, you have more bryophytes*". What was exciting about it is to have shown it with empirical data; a result which I hope will be useful for scientists in many ways, providing a valuable reference point for many future studies.

Altogether, I think I can draw some general conclusions from the work presented in this thesis: The number of species which occur in a local community (α diversity) is not necessarily influenced by regional diversity (species pool). The composition of these local communities however, is severely influenced by regional diversity. Both patterns only emerge at certain spatial scales and we need to understand better what mechanisms influence species diversity at what spatial scale.

Can I answer the question "What determines species diversity" yet? Yes and no - *yes* in part but not for every detail. Altogether I think this thesis answered some details of this overall question, and I hope it will have a lasting impact on the field of biogeography.

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PUBLIC OUTREACH

"Die Macht der Pflanzen", 27.04.2012, 20 Minuten

"Vielfalt auch auf kleinen Inseln", 17.02.2012, 20 Minuten

"Treffpunkt", Radiosendung, 21.02.2012, SRF 1

CONFERENCE TALKS

Karger, D.N., Amoroso, V.B., Darnaedi, D., Hidayat, A., Kluge, J., Abrahamczyk, S., Lehnert, M., Kessler, M. Biogeographical and ecological drivers of beta diversity across scale. Popbio 2012. 25th Annual Conference of the Plant Population Biology Section of the Ecological Society of Germany, Switzerland and Austria, 17th – 19th May 2012, Zurich, Switzerland. (best PhD-presentation).

Karger, D.N., Amoroso, V.B., Darnaedi, D., Hidayat, A., Kluge, J., Kessler, M. Patterns of Fern Diversity in the Southeast Asian Archipelago. International Biogeographical Society "Advances in Biogeography: Early Career Conference", September 23rd - 25th 2011, Oxford, UK.

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Karger, D.N., Patterns of Biodiversity: A Seminar on Ecology, 15th December 2010, University of Santo Tomas, Manila, the Philippines.

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Karger, D.N., Tuomisto, H., Amoroso, V.B., Darnaedi, D., Hidayat, A., Abrahamczyk, S., Kluge, J., Lehnert, M., Kessler, M. Beta diversity on tropical islands. The International Biogeography Society, 6th Biennial Conference, 9th-13th January 2013, Miami, USA.

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